Legume Nodulation

A Global Perspective

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To all my friends, students and colleagues of the last 50 years, but especially to my long-suffering husband Peter.

'Leguminosae are one of the great lines of dicotyledonous evolution. They far exceed the idea of an order or family except within the narrow confines of nomenclature. The neap tide of modern botany never uncovers its riches. Legumes invest our lives and a feeble backwash seeps through our universities' (Corner, 1976).

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Preface

Since publishing my book 'Nodulation in Legumes' in 2001, many people have kindly suggested that I write a second edition. For various reasons I have decided not to do this, but rather attempt to put nodulated legumes into a wider context.

In the last few years several major works have appeared that have made the writing of this book easier and to which I have extensively referred. Foremost amongst these is 'Legumes of the World', edited by Gwil Lewis and colleagues at Kew. In addition to the magnificent photographs of all legume genera, and descriptions of them, the volume has extensive biogeographical coverage. A series of books has been published by Springer on 'Nitrogen Fixation, Origins, Applications, and Research Progress', under the general editorship of Bill Newton, but with individual volumes having additional editors. Unfortunately the volumes had a rather long gestation period, so that although there is a vast amount of material in them that remains important, in some cases (for example, the bacteria known to nodulate legumes), there is a large body of more recent information. On the ecological side, several important volumes have been published, one of which, 'Neotropical Savannas and Seasonally Dry Forests', edited by Toby Pennington and colleagues, has a wealth of information on the distribution of legumes in these important ecosystems. Overall, the chapters in these various volumes, all of which are written by international experts, provide a level of detail that is not attempted here. Rather I have attempted to summarise current knowledge and go into detail of aspects that are less well covered.

In trying to put a more global perspective on legume nodulation, I have had several aims. The first is to demonstrate that nodulated legumes are found in all habitats and in nature do not conform to many of the rules accepted by agronomists. With current interest in global change and in protecting fragile ecosystems, it is important to realise what nodulated legumes can and cannot do. I have also tried to counter some of the widely quoted generalizations – for example, that tropical legumes have determinate nodules and export ureides (most have indeterminate nodules and export amides) and that the polymer of β-hydroxybuturate (PHB) is necessarily associated with bacteroids of such genera (I argue that it is a measure of inefficiency in bacteroids of nodules from many legumes).

Deciding on a logical order for the chapters was difficult. In the end I thought that it was best to start with the plant taxonomy to give an up-to-date picture of the distribution of nodulation within the family at a generic and tribal level, which has changed somewhat since my 2001 book. I have made no attempt to list all the non-nodulated

species, but have included all the known nodulated species in appendices, with an introductory 'health warning'. Species names, where possible, have been checked against the International Legume Database and Information Service (ILDIS), but for various reasons, particularly shortage of funding, parts of this are not entirely up to date and where this is the case, I have checked with relevant taxonomic experts. In this chapter I have also given a general indication of the types of bacteria that may nodulate various genera, but it is not possible to do this in a comprehensive fashion, as new reports are coming out regularly. It is planned to produce an electronic interactive database of this information when the current volume has gone to press. Chapter 2 covers some aspects of the global distribution of legumes, largely based on the biomes described in Schrire et al. (2005). Again there are a number of systems that are not covered, usually because of insufficient information being available. Chapter 3 outlines some of the current ideas on evolution of nodulation, based on a number of recent reviews. The bacteria currently known to nodulate legumes are described in Chapter 4. New species are coming out almost weekly, with several reports being in press as this book goes to press. In this chapter I have also emphasised that isolating bacteria from nodules is not sufficient to confirm nodulating ability; Koch's postulates must be established. Reports of nodulation in some legume genera (Chapter 1) and of bacteria purporting to nodulate legumes have not always been reliable, and I have tried to indicate where this might be the case. Chapter 5 attempts to put the plants and bacteria together, discussing nodule development and functioning, but without going into the detail given in major recent reviews and chapters in other volumes. At a late stage in the book's planning I decided to end with a short chapter on possible development of new uses for legumes and for more work on underdeveloped legume crops. In spite of the noble effort of the U.S. National Academy of Sciences, there is still an overemphasis on major economic crops such as soybean and peanut, whereas in many areas of the world, other legumes may be better adapted to the local environment and also be more acceptable to local people.

I have intentionally allowed some overlap in content between chapters, as I believe that this will make for easier reading for those wanting to concentrate on particular topics. Measurement of nitrogen fixation in the field is fraught with difficulties and in many areas effectively impossible. The fact that I have not attempted to do this does not mean that I do not think that legumes nodules do not have a vital role to play in nutrient cycling.

In recent years, there has been a tendency for both the legume and rhizobial fraternities to be isolated from each other. This has been an inevitable consequence of current research conditions and the need to publish in either highly specialised journals or in the top group of journals such as *Nature* and *Science*. This has had some unfortunate consequences, as journals tend to use referees with a rather narrow focus, in the case of nodulated legumes with either plant or microbial specialists who may not appreciate the other's disciplines. Some disciplines such as whole plant physiology and soil science have been neglected in favour of new molecular studies. Careful, old-fashioned fieldwork, especially in difficult terrains, gets few brownie points these days, as it may take years of work to produce a set of statistically significant data. However, with the recognition that the climate really is changing and that food supplies cannot be guaranteed, there is a move to bring people of different disciplines together. I hope that

this book may be of some help, by being comprehensible and sufficiently jargon free to interest soil microbiologists, plant physiologists, taxonomists and ecologists and well as agronomists. A basic understanding of biology is assumed and there are extensive references to the literature so that readers can indulge their interests in particular topics. To do justice to them all would have required a very large volume, so I have erred on the cautious side.

It is impossible without writing another book on the subject to thank the many people who have helped me over the years. Just to give an indication, at one end of the age scale is my old friend 'Tom' (H.D.L.) Corby, whose pioneering work on nodule morphology when he was working in what is now Zimbabwe inspired me and many others to expand on this topic. I still have Tom's collection of nodules and was delighted to catch up with him, now 95 and firing on all cylinders, in Cape Town in 2008. At the other end of the age scale I count the many young students, for example in Murdoch University in Western Australia, who are a joy to talk to. In between there are new contacts, working in some of the extreme conditions that so urgently need study, such as H.S. Gehlot, working in the Thar desert in India and Wenfeng Chen from Beijing working in the Qinghai Tibetan plateaux at 4000 to 5000 m and who, though I have not yet met them, have been generous in supplying information and photographs. More recently Ben-Eric van Wyk has introduced me to the wonderful world of South African legumes. I hope the hundreds more that I could have included will forgive their absence from this list, but I must mention Euan James, an unfortunate casualty of the reorganization of Life Sciences in Dundee, whose expertise and collaboration has been invaluable for years, but especially in recent research and publications. Euan and many others have generously supplied me with photographs, and my husband Peter constructed the diagrams. Kate Nuttall and Nigel Bamforth at Blackwell/Wiley have patiently coped with my various idiosyncrasies and steered the volume through its gestation period.

Plate 2.1 *Prosopis grandiflora* var. *torreya* growing on dunes in Death Valley, California, where the daytime temperatures can exceed 40°C. (Courtesy Peter Felker, Salinas, California.)

Plate 2.2 A species of *Acacia* in the dry season, having shed its leaves, near Lake Turkana, Northern Kenya.

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Plate 2.3 *Acacia aneura*, a phyllodinous species that retains its phyllodes in the dry season. Taken in a revegetation area following iron mining in the North of Western Australia. See also Plate 5.3.

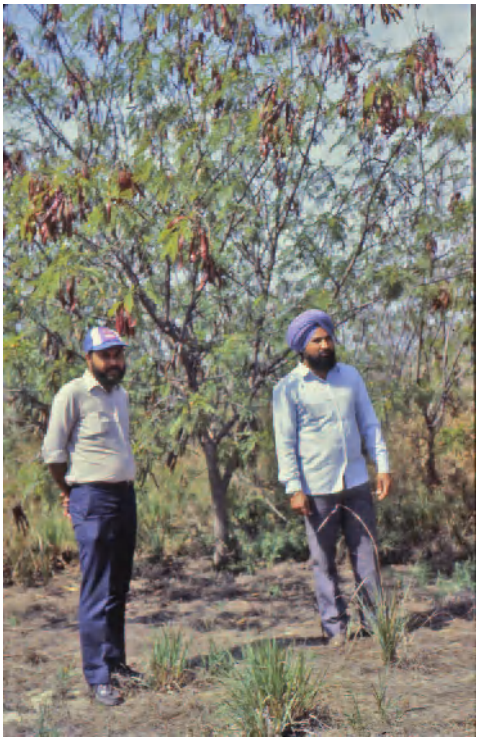

Plate 2.4 *Leucaena leucocephala* growing well on a sodic soil in Karnal, India, at the Central Salinity Research Insitute. Note the abundant production of seed, which has led to this species becoming invasive in some areas of the world.

Plate 2.5 A typical savanna area in Kenya, found also in many other parts of East and Southern Africa. The land is usually flat and heavily grazed by native herbivores or by goats. The nodulated legume tree is *Acacia tortilis*, which occurs widely in drier parts of Africa.

Plate 2.6 General view of Cerrado vegetation. This area is much more hilly and rocky than the corresponding area of Kenya (Plate 2.5) and is not grazed by large herbivores. (Courtesy Euan James, Dundee.)

Plate 2.7 Nodulated *Chamecrista nictitans* in the Cerrado area of Brazil, showing large xylopodium, typical of many of the plants that grow there and which enables them to regenerate after fire.

Plate 2.8 Caatinga vegetation. Superficially this resembles Cerrado, but the rainfall pattern and species composition is different. (Courtesy Euan James, Dundee.)

Plate 2.9 Typical pea-flowered Australian legume, found in the southwest of Western Australia.

Plate 2.10 Cape florisitic region of South Africa, showing typical shrubby vegetation. There are few grasses and the yellow flowering plants are species of *Cyclopia*, harvested for production of honeybush tea.

Plate 2.11 A commercial field of *Aspalathus linearis*, being grown for production of rooibos tea. This field is also in the Cape Floristic region and the very poor nature of the soils is clear.

Plate 2.12 The Tibetan plateau, which averages 4500 m in height. It is heavily grazed, but some legumes, such as the *Caragana* species shown here, survive and prosper. (Courtesy, B.C. Hou and Wenfeng Chen, Beijing.)

Plate 2.13 **A,** *Lupinus nubicus* growing at 4950 m in the Peruvian Andes. **B,** detail of plants. **C,** detail of nodules. Note the heavily pigmented (haemoglobin) interior of the nodules and the classic lupinoid morphology, with nodules growing around the root. The infected region of the nodules shows a number of discreet portions, corresponding to separate infection events. (Courtesy Colin Hughes, Oxford.)

C

Plate 2.13 (*Continued*)

Plate 2.14 *Lupinus nootkanensis* (blue colour) invading a large area of natural vegetation in Iceland.

Plate 5.1 Plant of *Aeschynomene afraspera* growing in Senegal. Rows of stem nodules can be seen on most branches.

Plate 5.2 *Sesbania rostrata* from a trial ground at the International Rice Research Institute in the Philippines, where its value as a green manure for rice growing is assessed. **A**, plants growing in flooded plots; **B**, detail of nodules forming along the stem. (Courtesy Euan James, Dundee.)

Plate 5.3 *Centrosema* sp. on mine spoil from iron mining activity near Belo Horizonte, Brazil. **A**, plant growing alongside a large piece of iron ore; **B**, nodules on roots near the soil surface, among the leaf litter.

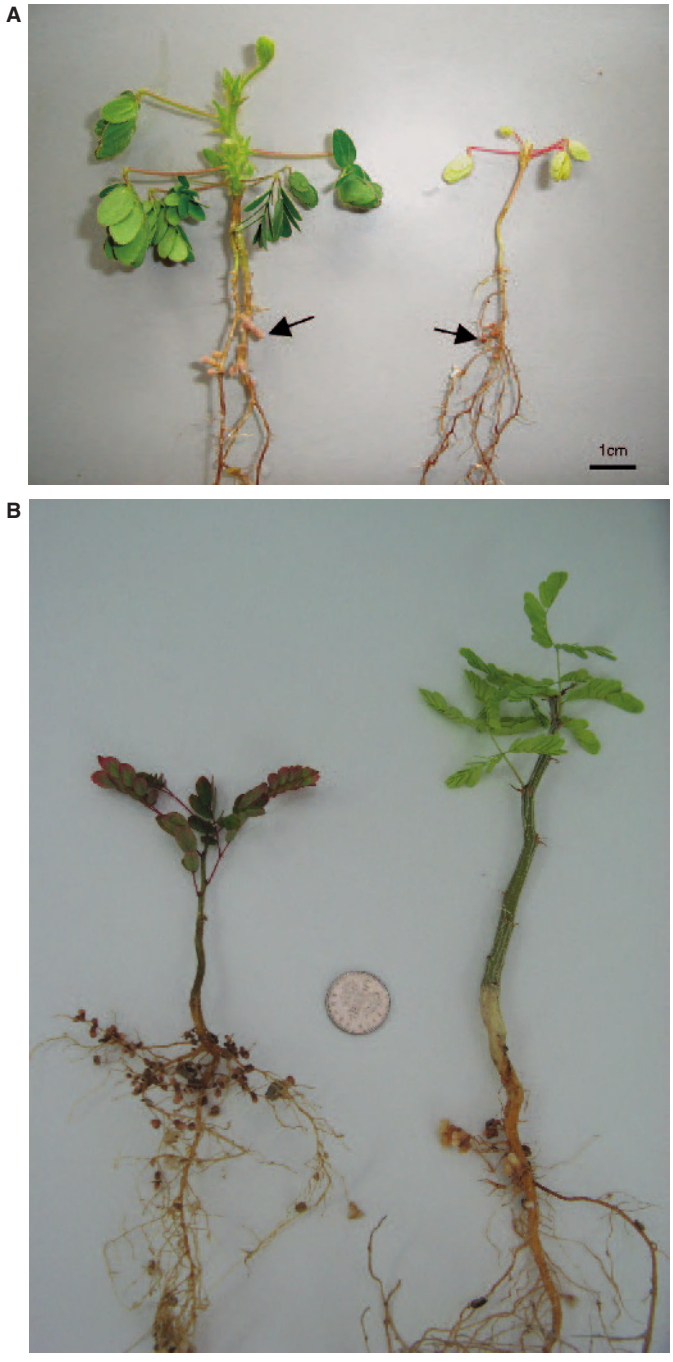

Plate 5.4 Examples of ineffective nodules. **A**, *Mimosa ursina* inoculated with *Burkholderia phymatum* (left) and *Cupriavidus taiwanense* (right). Both plants nodulated (arrows), but only the ones of the left-hand plant were effective. (Courtesy Euan James, Dundee.) **B**, two different species of mimosoid legume, inoculated with *B. phymatum*; *Leucaena multicapitula* (left) and *Acacia senegal* (right). Both nodulated, but the nodules on the acacia were ineffective, although the plants appear quite healthy at this stage. **C**, *Acacia farnesiana* nodule halves showing typical variations in internal colour, with the darker pink one being more effective than the lighter pink one and the green one being typical of some completely ineffective nodules, but also seen in senescent nodules. (Courtesy Joan Sutherland, Dundee.)

C

Plate 5.4 (*Continued*)

Plate 6.1 **A,** *Vigna subterranea* (bambara groundnut) field trial in Botswana. **B**, details of plant to show subterranean pods. (Courtesy Shravani Basu, University of Nottingham.)

Plate 6.2 Cowpea growing with maize in a field trial in South Africa.

Plate 6.3 Edible tubers on *Vigna vexillata*. (Courtesy Bob Lawn, Townsville.)

Plate 6.4 Well-nodulated root of *Vigna unguiculata* (cowpea) grown in South Africa

Plate 6.5 Tubers of *Pueraria tuberosa* with nodulated roots. (Courtesy H.S. Gehlot, India.)

Plate 6.6 *Erythrina edulis* from plants grown in the Peruvian Andes. (Courtesy Colin Hughes, Oxford.)

Plate 6.7 *Lebeckia ambigua*, which is being developed as a drought-resistant forage legume for use in acid soils. **A**, woody root (cf Plate 2.6) enabling plants to resist grazing and drought; **B**, plants growing on a farm in Nieuwartdville, Western Cape, South Africa. (Courtesy John Howieson, Perth.)

Plate 6.8 *Sutherlandia frutescens* (cancer bush) in its native habitat in South Africa.

Plate 6.9 Factory for the production of rooibos tea, in Clanwilliam, South Africa. Note the large area to the left of the factory, where harvested shoots are laid out to dry.

I took this aerial photograph some years ago in the mid-west farming region of the USA. The entire landscape is covered by fields of light green corn (maize) and dark green soybeans. As soybean producers pay a levy on their crop, much of which goes into research, it is not surprising that the literature on nodulation and nitrogen fixation by soybeans exceeds that on any other single legume crop.

Chapter 1

Nodulation in a Taxonomic Context

In 2005, Lewis et al. published their comprehensive and beautiful book 'Legumes of the World', in which all genera then known are described and at least one species of each illustrated. In addition, the book contains a very interesting account of legume biogeography, which will be the subject of Chapter 2. The general terminology of Lewis et al. (2005) will be followed here, i.e. the family Leguminosae (or Fabaceae as some prefer) is divided into three sub-families, each of which is divided into tribes. Table 1.1 summarises these tribes and the numbers of genera and species within them. Since, with a very few known exceptions, detailed where appropriate, nodulation is a generic characteristic, for the purposes of the following discussion all species within a genus are presumed to nodulate, even though the number recorded as nodulated may be far less than the total (Tables 1.4 to 1.17). At various times when genera have been divided, it has unwittingly also been on presence or absence of nodulation (Table 1.2). Many of the more recently described genera in sub-families Mimosoideae and Papilionoideae have been segregated from others that can nodulate, but often there is no information on the nodulation status of the new combinations. Whilst, because of their taxonomic position, many of these are likely to be able to nodulate, in view of the examples given in Table 1.2, it certainly cannot be taken for granted.

In all three sub-families, there is active research on tribal and generic details. The authors of the various chapters in Lewis et al. (2005) present the current situation as they see it, pointing out anomalies without taking a position, because one of their aims is to stimulate research. In this sense, their book can be described as covering 'work in progress'. In some cases nodulation characteristics may add some clarity, and this will be attempted in the present chapter. A further complication is that the current ideas of taxonomy, phylogeny and evolution are not entirely congruent with known major alterations in the chloroplast genome. Doyle (1995) outlined the major changes of importance for legumes, of which two are relevant here. Chronologically the first is the inversion of a 50kb section of chloroplast DNA. This is absent from Caesalpinioideae and Mimosoideae, but present in most Papilionoideae. The second is the loss of a large duplicated and inverted section of the genome, present in nearly all land plants, and known as the inverted repeat (IR). Liston (1995) carried out an extensive survey of this feature of legumes, which is largely confined to the more advanced papilionoid

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Table 1.1 Summary of tribes, genera and species in the three subfamilies of Leguminosae, mainly as given in Lewis et al (2005), except that Mimozygantheae is included here in Mimoseae and some recent changes in Crotalarieae are included. Numbers of species are approximate

Caesalpinioideae			
Tribe	Genera	Species	Comments
Caesalpinieae	56	429	7 gen. known to nodulate 171 spp.
Cassieae	21	73	One nodulating genus 330 spp.
Cercideae	12	335	May be a separate branch
Detarieae	82	747	None known to nodulate
Mimosoideae			
Tribe			
Acacieae	1	1450+	Subdivision in hand
Ingeae	36	950	~300 in *Inga*
Mimoseae	41	870	~500 in *Mimosa*
Papilionoideae			
Tribe			
Abreae	1	17	
Amorpheae	8	246	165 in *Dalea*
Bossiaeeae	6	72	
Brongniartieae	10	151	
Cicereae	1	43	
Crotalarieae	12	1120	Subject to revision
Dalbergieae	49	1324	250 in *Dalbergia*
Desmodieae	30	527	275 in *Desmodium*
Dipterygeae	3	22	Non-nodulating
Euchrestieae	1	4	
Fabeae	5	328	Formerly Vicieae
Galegeae	24	2929	2300+ in *Astragalus*
Genisteae	25	561	225 in *Lupinus*
Hedysareae	12	426	140–180 in *Hedysarum*
Hypocalypteae	1	3	
Indigofereae	7	768	700 in *Indigofera*
Loteae	22	282	Includes Coronillieae
Millettieae	45	908	350 in *Tephrosia*
Mirbelieae	25	687	
Phaseoleae	89	1576	230 in *Rhynchosia*
Podalyrieae	8	125	
Psoraleae	9	185	
Robinieae	11	71	
Sesbanieae	1	60	
Sophoreae	45	295	Polyphyletic
Swartzieae	17	258	Polyphyletic
Thermopsideae	6	45	
Trifolieae	6	425	

Table 1.2 Generic changes that have unwittingly included nodulation. Nodulating genera in bold type. They include one genus from each sub-family

Old genus	New genera	Reference
Cassia	*Cassia, Senna,* ***Chamaecrista***	Irwin & Barneby, 1982
Newtonia	*Newtonia,* ***Pseudopiptadenia***	Lewis & Lima, 1991
Sophora	***Sophora,*** *Styphnolobium*	Sousa & Rudd, 1993

tribes, but which also occurs in some others, causing some difficulties for classification, discussed later. As each of these two changes is thought to have occurred only once, it is hoped that when more genera have been analysed for them, their presence/absence will help clarify some anomalies. Although very important for legume phylogeny, there are no known nodulation characteristics involved in these chloroplast genome changes (or, indeed, in the chloroplast genome at all).

In the following sections, brief reference will be made to nodule morphology and structure (Figs. 1.1 and 1.2), and to the bacteria inducing nodules, detailed in Chapter 4. Basically, bacteria nodulating legumes are known collectively as rhizobia, and they fall within several families of two branches (α and β) of phylum Proteobacteria. Earlier they were often categorised in terms of fast or slow growth and these terms will also be used here.

1.1 Caesalpinioideae

This sub-family has long been known to contain the smallest proportion of nodulated species (Allen & Allen, 1981). However, it is worth re-examining the distribution of nodulation in the light of currently described tribes. Cercideae and Detarieae are basally branched from the rest of Caesalpinioideae (Fig. 1.3): neither has known nodulated members and Detarieae is uniformly ectomycorrhizal. Most legumes are arbuscular mycorrhizal (AM) or, in some cases, have both types. Tribe Cassieae has one nodulating genus, *Chamaecrista*. However, this has 330 species, a significant number of which have been recorded as nodulated and none as non-nodulated. This genus represents nearly half the species in the tribe. Further, sub-tribe Cassiinae, which contains *Chamaecrista*, appears to fall within the confines of tribe Caesalpinieae (Lewis, 2005a; Fig. 1.3), which contains all other known nodulating genera. Caesalpinieae has been divided into a number of groups, some of which contain only non-nodulating genera. Nodulated genera are scattered among several groups, with no apparent logic. In a more recent study, Bruneau et al. (2008) sampled all but one of the caesalpinioid genera, but with varying levels of rigour because of the availability and quality of DNA. This analysis clarified the relations among many of the genera. Unfortunately the nodulated genera remain scattered and the hope expressed by Haston et al. (2005) that, with the inclusion of more molecular characteristics, the nodulating genera may emerge as more closely related than generally thought has not yet been fulfilled. One generic change

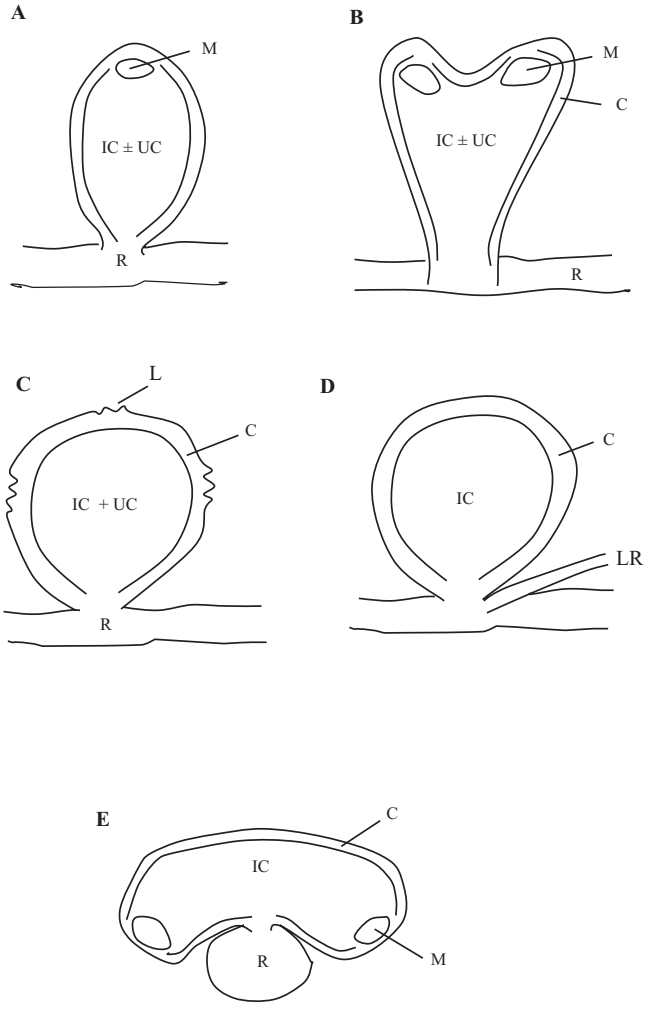


Figure 1.1 The arrangement of tissues in the major types of nodule. **A** and **B** are indeterminate forms (see also Fig. 1.2C), with a single or a branched apical meristem. Nodules that appear similar in morphology may have uniform infected tissue or a mixture of infected and uninfected cells, according to taxonomic position. **C**, desmodioid (determinate) nodule (Fig. 1.2A), with infected tissue always containing uninfected cells. **D**, aeschynomenoid nodule as found in legumes from the Dalbergioid clade. These are always associated with lateral or adventitious roots and have uniform infected tissue. **E**, a variant of an indeterminate nodule containing only infected cells in the infected region, but with two lateral meristems, resulting in a 'collar' or lupinoid nodule that encircles the subtending root (occasionally stem). Only known from a few Genistoid legumes. (M, meristem; C, nodule cortex, containing vascular tissue; R, subtending root; LR. lateral root; IC infected cells; UC uninfected cells.) (Modified from Sprent, 2007.)

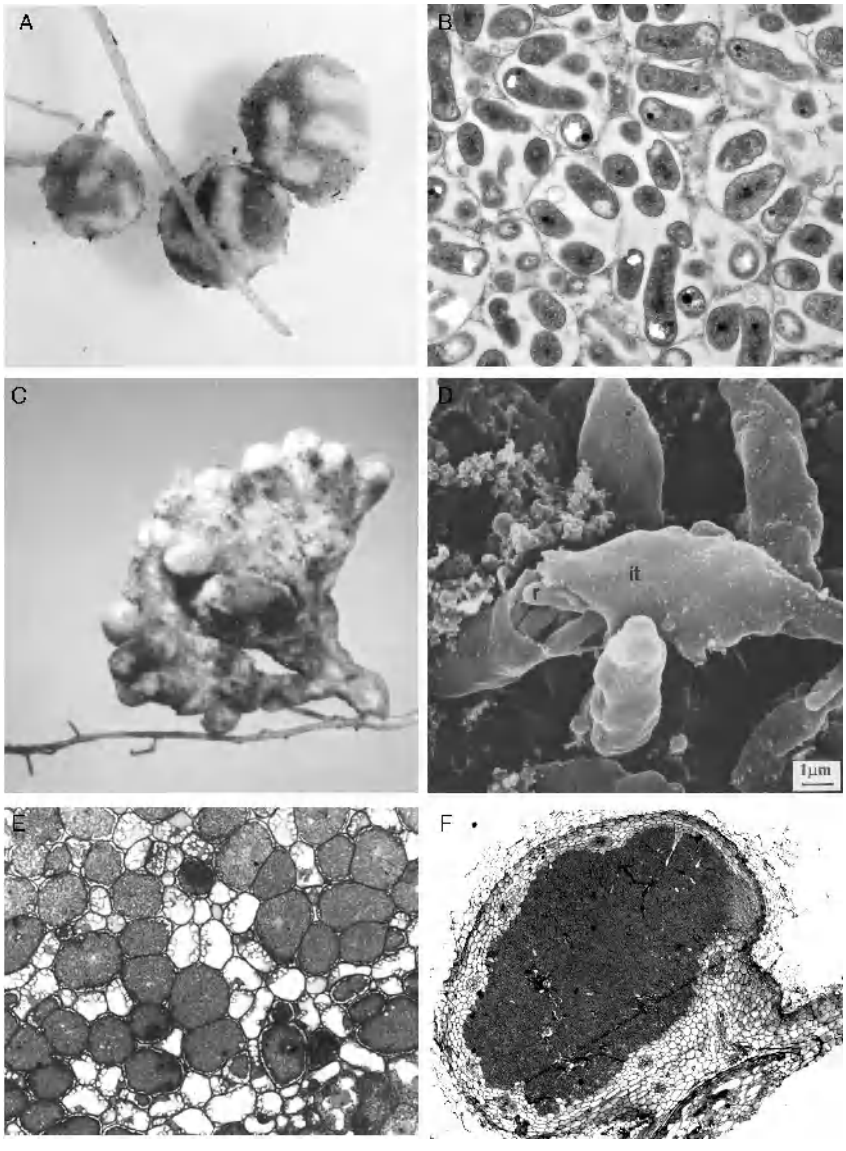
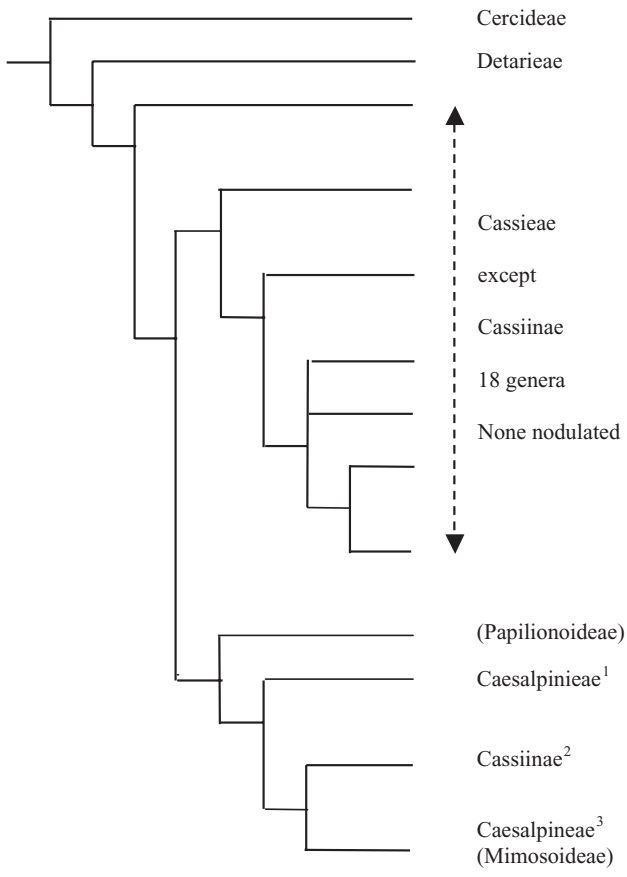


Figure 1.2 Major types of legume nodule. **A**, desmodioid nodule as found in the phaseoloid tribes (Table 1.15, and some members of tribe Loteae (Table 1.16). Lenticels are characteristic. Nodules vary from 2 to 5 mm in diameter and the infected tissue contains both infected and uninfected cells (Fig. 1.1C). **B**, symbiosomes; these membrane-bound structures may contain 1 to 8 bacteroids (the nitrogen-fixing form of rhizobia). **C**, a much-branched indeterminate nodule, as found in many species from all three subfamilies. Other indeterminate nodules may be much less branched or unbranched, and the infected tissue may contain only infected cells or a mixture of infected and uninfected cells (Fig. 1.1A, B), a taxonomic characteristic. Size varies from 3 mm to several cm in length. **D**, a broken modified infection thread (IT), often called a fixation thread, showing bacteroids. This is considered a primitive state in which bacteria are not released into symbiosomes and is found in caesalpinioid and some papilionoid nodules. **E**, infected tissue containing a mixture of infected (darkly stained) and uninfected cells (see Fig. 1.1). **F**, infected tissue containing only infected cells. Infected cells in either **E** or **F** arrangements may be highly vacuolate in some species. (From Sprent, 2007.)



[1] Pro parte; 7 genera, none nodulated

[2] 3 genera, including *Chamaecrista*

[3] Pro parte; 49 genera, including all 7 nodulated ones

Figure 1.3 Possible relationships between nodulated and non-nodulated groups in the Caesalpinioideae. The position of Papilionoideae in this diagram can be ignored. (After Lewis, 2005a.)

since Sprent (2001) is that *Sclerolobium* has been incorporated into *Tachigali*. Both can nodulate, although this was not one of the properties used in the reclassification. The seven genera known to nodulate (*Campsiandra, Chidlowia, Dimorphandra, Erythrophleum, Melanoxylon, Moldenhawera* and *Tachigali*) account for 171 of the 429 species in tribe Caesalpinieae. Again, this is a significant proportion, equal or exceeding that in some tribes of the Papilionoideae. All nodulating caesalpinioid genera, except *Chidlowia*, a monotypic genus from tropical Africa, and *Erythrophleum*, which is found in Africa and Australia, together with some herbaceous pan-tropical species of *Chamaecrista*,

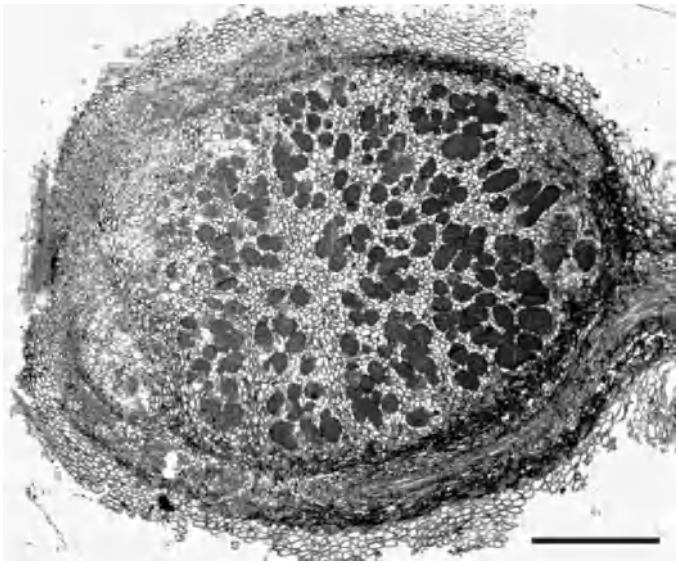


Figure 1.4 Longitudinal section of a typical caesalpinioid nodule, showing the characteristic blunt apex and infected tissue with a mixture of infected and uninfected cells. In some species nodules may branch and be lignified in the outer layers. Infected cells have bacteroids retained in fixation cells (Fig. 1.2D). Bar = 500 μm. (Courtesy of E.K. James.)

are from South America. All, excepting herbaceous species of *Chamaecrista*, have their nitrogen-fixing bacteria retained with modified infection threads, known as fixation threads (Fig. 1.2D). The evolutionary implications of these aspects of caesalpinioid legumes will be considered in Chapter 3. All nodules show indeterminate growth, are often branched and may be quite woody. The tips of nodules are usually flattened, and the infected tissue contains both infected and uninfected cells (Fig. 1.4).

Very little is known about the bacteria nodulating caesalpinioid legumes. The only species in commercial use, as a forage plant, is *Chamaecrista rotundifolia,* marketed in Australia as Wynn Cassia. The commercial inoculant for this is a broad-range strain of *Bradyrhizobium*, CB756 (A. McInnes, personal communication). *Ch. fasciculata* was the only caesalpinioid legume found to nodulate with the fast-growing, wide host range strain NGR234 (Pueppke & Broughton, 1999). Parker (2008) found that all 20 isolates from nodules of *Tachigali versicola* were bradyrhizobia and we have evidence that *Chamaecrista nictitans* nodules collected in the field in Brazil house a species of *Burkholderia* (E.K. James, personal communication).

1.2 Mimosoideae

In terms of genera, but not species, Mimosoideae is the smallest of the sub-families. (Table 1.1). Former tribes Parkieae and Mimozygantheae are now included in Mimoseae

(in Lewis et al., 2005, Mimozygantheae is retained). All tribes are due for changes, the most comprehensive of which are in Acacieae, which contains the single genus *Acacia*.

Nodules in all mimosoid legumes studied are indeterminate, but vary considerably in morphology and whether or not they are branched. Structurally, none is known to have bacteroids retained within infection threads as they are in most Caesalpinioideae and some Papilionoideae. This is interesting in view of the possible position of Mimosoideae with respect to Caesalpinioideae in Fig. 1.3 and will be explored further in Chapter 3.

1.2.1 Acacieae

In Lewis (2005b), tribe Acacieae has one genus, *Acacia*. It has been known for decades that *Acacia* is not monophyletic, and for many years it has been divided into three sub-genera, *Acacia*, *Aculeiferum* and *Phyllodineae* (also called *Heterophyllum*). Generic names have been suggested for these, but not widely accepted. This may be just as well as it now appears that there should be at least five genera arising out of *Acacia*. These are listed in Table 1.3. In Lewis (2005b), the *A. coulteri* group is referred to as 'genus X'. This has now been named *Mariosousa* (Seigler et al., 2006). As well as the number of genera being in doubt (more may yet be added) the tribal affinities remain unclear. The suggestions in Table 1.3 may be altered when more taxa are sampled, but it is interesting that species of the seed-predating bruchid beetles support this tribal arrangement (Kergoat et al., 2007). If further evidence supports the divisions given in Table 1.3, then tribe Acacieae will cease to exist. Added to the scientific confusion are considerations of national pride. Many Australians regard acacias as part of their natural heritage, even though they usually refer to them as wattles, and wish to use the generic name *Acacia* for sub-genus *Phyllodineae*. Others, including some Australians, believe that the usual procedures should be followed, in which case sub-genus *Acacia* should retain that name. For this reason the old terms have been retained in Table 1.3. However, the subdivisions there have significance for symbiotic properties, which is why the controversy over terminology has been engaged, rather than opting for a quiet life!

Table 1.3 Possible sub-division of *Acacia* into five genera and re-assignment into tribes. Based on Maslin et al. (2003), Seigler et al. (2006) and Rico-Arce (2007)

Sub-genus	Species	Geographical range	Tribe?
Acacia	161	Mainly Africa and South America, some in Asia and Australia	Mimoseae
Aculeiferum	203	Section Aculeiferum. Africa, Asia, Section Monacanthea, pan-tropical	Ingeae
Acaciella	14	reinstatement of an old genus for *Aculeiferum*, section Filicinae New World	
Mariosousa	13	*A. coulteri* group, New World	
Phyllodineae	~960	Mainly Australia, some Asia	Ingeae

Sub-genus *Phyllodineae* is the only one that has members with both ecto- and arbuscular mycorrhizas, a feature that makes them very good for land reclamation and also for becoming invasive. When *Phyllodineae* is further subdivided, it may be that only certain sections have this attribute (Sprent, 1994a). Species can nodulate with a wide range of rhizobia (Lafay & Burdon, 2001, chapter 4), but *Phyllodineae* is the only sub-genus to nodulate effectively with the wide host range strain NGR234 (Pueppke & Broughton, 1999). Nodulation appears to be a generic characteristic. Leary et al. (2006a) cite two species that were reported not to nodulate, but these observations have not been confirmed and probably reflect conditions when samples were collected. Nodulation also appears to be generic for sub-genus *Acacia*, but not for *Aculeiferum*, which has two sections, Aculeiferum, found in Africa and Monacanthea, which is pan-tropical. So far 16 species of the latter section, from both Africa and America, have been found unable to nodulate (Sprent, 2001). Proving a negative is always difficult, but these species have been extensively studied and also form a very close group on molecular characteristics. It is likely that they have lost the ability to nodulate, rather than never having had it. The bacteria nodulating sub-genera *Acacia* and *Aculeiferum* vary greatly as does their effectiveness in fixing nitrogen. These aspects will be examined in more detail in Chapters 2 and 5.

1.2.2 Ingeae

Tribe Ingeae, apart from including at least sub-genus *Phyllodineae* from the Acacieae, currently consists of 36 genera, dominated in species by *Inga* (300) and *Calliandra* (135) (Table 1.4). The monospecific genus *Faidherbia* was for many years called *Acacia albida*. Because it is widespread in Africa and has some unusual properties, such as shedding its leaves in the wet season and producing them in the dry season, it has been the subject of much research. Most members of Ingeae occur in the New World, but with several in Africa (including Madagascar), Asia and Australia. Recent evidence suggests that the Australian and SE Asian genera are closely related (Brown et al., 2008). There are 10 genera (48 spp.) for which there is no information on nodulation status. These include *Viguieranthus*, many of whose species were formerly included in *Calliandra*. *Zapoteca*, on the basis both of a few field observations and of laboratory studies, has not yet been found to possess nodules. This is the only genus in the tribe with negative reports on nodulation and more information is urgently needed.

Members of Ingeae are nodulated by a wide range of rhizobia, including some *Burkholderia* spp. (Chapter 4). The most widely studied genera for their nitrogen-fixing properties are *Albizia, Calliandra* and *Inga. Albizia* spp. are important shade trees, especially for cocoa, in large parts of Africa. *Calliandra calothysus* is widely used in agroforestry in Africa, where it is preferred to other woody legumes such as *Leucaena* because it seeds less freely and therefore does not become a weed. Although native to Central America, it nodulates with a range of rhizobia wherever it is grown (Bala & Giller, 2001). *Inga* species are also used as nurse and shade crops, the latter often for coffee in South and Central America. All species have edible fruits and many, for example *Inga edulis*, are grown for this reason. These and many other uses of *Inga* species are described in the monograph by Pennington and Fernandez (1998). *Inga* spp. are very important in some ecosystems (Chapter 2).

Table 1.4 Known nodulation of genera (as in Lewis et al., 2005), in tribe Ingeae

Genus	Species	Nod.
Abarema Pittier	46	13
Albizia Durazz	120–140	46
Archidendron F. Muell.	94	6
Archidendropsis F. Muell.	14	2
Blanchetiodendron Barneby & Grimes	1	?
Calliandra Benth.	~135	25
Cathormium (Benth.) Hasske.	1	?
Cedrelinga Ducke	1	1
Chloroleucon (Benth.) Britton & Rose	10	4
Cojoba Britton & Rose	12	1
Ebenopsis Britton & Rose	3	2
Enterolobium Mart.	11	8
Faidherbia A. Chev.	1	1
Falcataria (Nielsen) Barneby & Grimes	3	1
Guinetia L. Rico & M. Sousa	1	?
Havardia Small	5	2
Hesperalbizia Barneby & Grimes	1	1
Hydrochorea Barneby & Grimes	3	3
Inga Mill.	~300	63
Leucochloron Barneby & Grimes	4–5	?
Lysiloma Benth.	8–9	4
Macrosamanea Britton & Rose	11	3
Marmaroxylon Killip	9–13	?
Painteria Britton & Rose	3	?
Pararchidendron I.C. Nielsen	1	?
Paraserianthes I.C. Nielsen[1]	1	1
Pithecellobium Mart.	18	6
Pseudosamanea Harms	2	1
Samanea Merr.	3	2
Serianthes Benth.	~18	2
Sphinga Barneby & Grimes	3	?
Thailentadopsis Kosterm	3	?
Viguieranthus Villiers	~23	?
Wallaceodendron Koord.	1	1
Zapoteca H.M. Hern.	20	0?
Zygia P. Browne	45–50	10

[1] The number of species listed in both ILDIS and GRIN is 3, but there is only one in Lewis et al. (2005).

1.2.3 Mimoseae

Tribe Mimoseae is very complex and has many interesting features with respect to nodulation. Of its 41 genera, 9 appear unable to nodulate, 22 can and there is no information for the remaining 10 (Table 1.5). One, *Piptadenia*, has recently been divided into three (Jobson & Luckow, 2007), but not all new combinations are yet available. However, enough are to know that at least one species of each genus can nodulate. An

Table 1.5 Nodulation status of genera in tribe Mimosae, after Lewis et al. (2005) except that *Piptadenia* has been divided into three genera, after Jobson & Luckow (2007). One, formerly *Piptadenia viridiflora*, has yet to be assigned a generic name

Genus	Species	Nod.	Not-nod.
Adenanthera L.	13	0	5?
Adenopodia C. Presl.	~7	?	1
Alantsilodendron Villiers	10	?	?
Amblygonocarpus Harms	1	0	1
Anadenanthera Speg.	2	1	
Aubrevillea Pellegr.	2	?	?
Calliandropsis H.M. Hern. & P. Guinet	1	?	?
Calpocalyx Harms	11	0	1
Cylicodiscus Harms	1		1
Desmanthus Willd.	~24	4	0
Dichrostachys (DC) Wight & Arn	14	2	0
Dinizia Ducke	1	1	
Elephantorrhiza Benth.	9	4	0
Entada Adans.	~28	10	0
Fillaeopsis Harms	1	?	?
Gagnebina Neck ex DC.	8	?	?
Indopiptadenia Brenan	1	?	?
Kanaloa Lorence & K.R. Wood	1	?	?
Lemurodendron Villiers	1	?	?
Leucaena Benth.	22	17	0
Microlobius C. Presl.	1	1	
Mimosa L.	530+[1]	117	0
Mimozyganthus Burkart	1	1	
Neptunia Lour.	12	5	0
Newtonia Baill.	15	0	3
Parapiptadenia Brenan	6	3	0
Parkia R. Br.	~34	0	15
Pentaclethra Benth.	3	1	1
Piptadenia Benth.	23	6	0
Piptadeniastrum Brenan	1	1	
Piptadeniopsis Burkart	1	?	?
Pityrocarpa (Benth.) Britton & Rose	3	2	0
Plathymenia Benth.	1	1	
Prosopidastrum Burkart	~5	?	?
Prosopis L.	~44	19	0
Pseudopiptadenia Rauschert	11	2	0
Pseudoprosopis Harms	7	?	?
Schleinitzia Warb. ex Nevling & Niezgoda	4	2	0
Stryphnodendron Mart.	30	6	0
Tetrapleura Benth.	2	0	2
Xerocladia Harv.	1	1	
Xylia Benth.	9	0	4

[1] M. Simon, personal communication.

unusual feature is that *Pentaclethra*, which has three species, has at least one that can and one that cannot nodulate. There are many negative reports for *P. macrophylla* (African) and several positive reports for *P. macroloba* (South American). There are no reports for the third species, *P. eetveldeana* (African). Of the other non-nodulating mimosoid genera, most are African. As several of the genera whose nodulation status is unrecorded are grouped with known non-nodulating genera, it is likely that the proportion of non-nodulating genera will increase. Where they stand in possible evolutionary terms will be discussed in Chapter 3.

The largest genus in Mimoseae is *Mimosa*, with over 500 species, of which 115 are now known to nodulate (Elliott et al., 2008). Many of these nodulate with β-rhizobia (*Burkholderia* and *Cupriavidus*), rather than α-rhizobia, a topic that will be discussed further in Chapter 4. Elliott et al. (2007a) looked at the ability of genera related to *Mimosa* to nodulate with β-rhizobia and found no coherent pattern. The next largest genus, *Prosopis*, nodulates with a variety of α-rhizobia, but some species can also use β-rhizobia (James et al., unpublished data). Many of its species are highly drought and salinity tolerant and have interesting physiological properties such as bringing up water from deep in the soil (hydraulic lift). These properties are considered in Chapters 2 and 5. *Neptunia* has been quite widely studied because of the aquatic habitat of many of its species. Its species nodulate with a range of α-rhizobia (Chapter 4) from different genera.

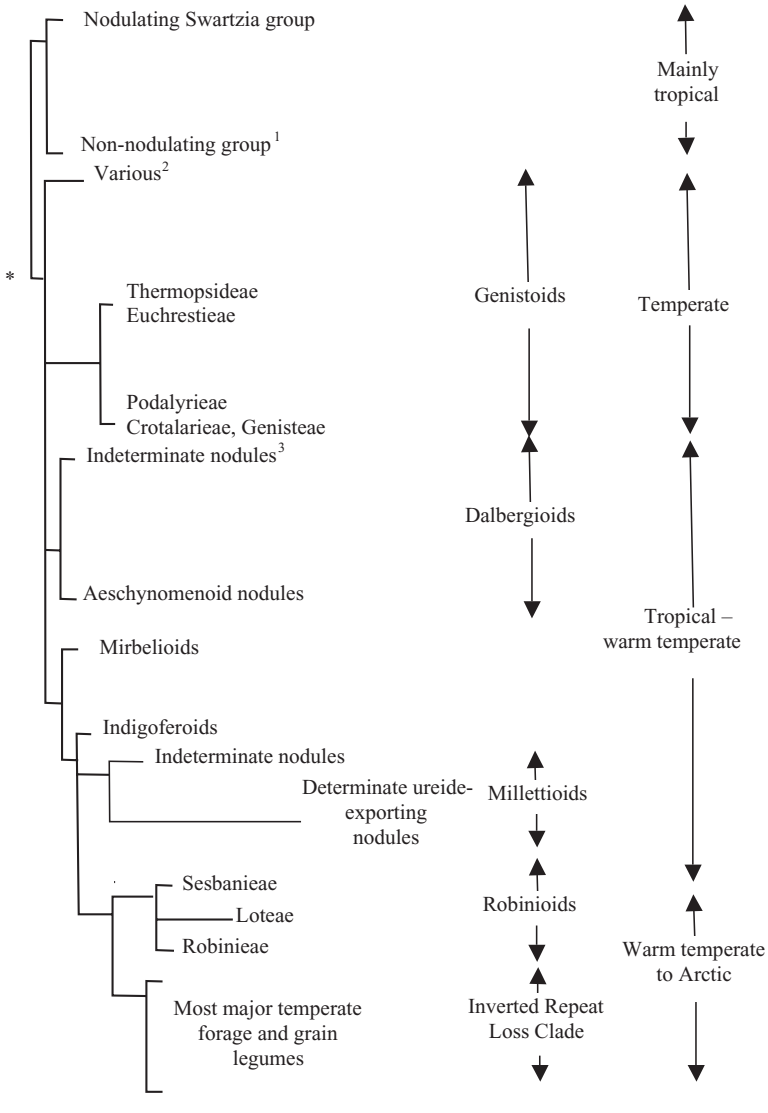
1.3 Papilionoideae

Papilionoideae is the largest and most complex of the three sub-families. For the present purpose, it has been subdivided on characteristics related to nodulation, nodule structure and nodule physiology. Fig. 1.5 outlines the major groups.

1.3.1 Non-nodulation in the Papilionoideae

As with Mimosoideae, some genera appear never to have had the ability to nodulate, whilst in others this ability may have been lost (as in some species of *Acacia*, sub-genus *Aculeiferum*). This section will deal with genera thought to be in the first category.

Three tribes of papilionoid legumes contain genera that appear to be unable to nodulate, namely Dipterygeae, Sophoreae and Swartzieae (the non-nodulating branch coupled to the nodulating Swartzia group in Fig. 1.5). The last two of these tribes also contain nodulating genera, and these are listed in Table 1.6. Tribe Swartzieae currently consists of 17 genera, but this number is likely to change as it is known not to be monophyletic and was even once thought to belong in the Caesalpinioideae. Of the 13 genera not listed in Table 1.6, there is no information on four, one (*Bocoa*) has mixed reports, with the remaining eight (*Aldina, Amburana, Baphiopsis, Cordyla, Exostyles, Harleyodendron, Mildbraediodendron,* and *Zollernia*) having good evidence of non-nodulation (Sprent, 2001). The latter group has a total of 41 species. Ireland (2005) put the four nodulating genera, together with *Bocoa, Candolleodendron* and *Trischidium*, in one



* 50 kb inversion

[1] Members of tribes Swartzieae, Dipterygeae, Sophoreae

[2] Members of Sophoreae, Dalbegieae and others, mainly non-nodulating

[3] Amorpheae + some 'old' dalbergiods, not included in Lavin et al. (2001)

Figure 1.5 Positions of the major groups of nodulating legumes in the Papilionoideae. (Modified from Sprent, 2007.)

Table 1.6 Known nodulating members of tribes Swartzieae and Sophoreae

Tribe Genus	Species	Nod.
Swartzieae		
Ateleia (DC) Benth.	20	5
Bobgunnia J.H. Kirkbr. & Wiersema	2	1
Cyathostegia (Benth.) Schery	1	1
Swartzia Schreb.	~180	27
Sophoreae		
Acosmium Schott.	17	3
Baphia Afzel. ex Lodd.	47	7
Bolusanthus Harms	1	1
Bowdichia Kunth.	2	2
Cadia Forssk.[1]	7	2
Calia Berland.	4	2
Clathrotropis (Benth.) Harms	6	3
Diplotropis Benth.	12	4
Maakia Rupr.	~8	1
Ormosia G. Jacks.	~130	26
Pericopsis Thwaites	4	3
Sophora L.	~50	15

[1] Boatwright et al. (2008a) suggest that this genus might be better placed in tribe Podalyrieae.

branch of the tribe, which may eventually become the tribe in its entirety. Since the last two of these genera are segregates from *Swartzia*, and since evidence for *Bocoa* is equivocal (Sprent, 2001), more observations are urgently needed to see if this branch is a nodulating one, a suggestion that is strongly supported by the detailed analysis of Torke and Schaal (2008), who placed these genera, plus *Fairchildia panamensis* (formerly *Swartzia panamensis*, with no record of its nodulation) in a core Swartzioid clade. In Ireland (2005) the non-nodulating genera together with the unknown ones *Holocalyx* and *Lecointea* form three separate groups interspersed among parts of the Sophoreae. Tribe Sophoreae is also in a rather chaotic state and has been known for many years not to be monophyletic. In Pennington et al. (2005) it has 45 genera, 12 of which are known to nodulate (Table 1.6). Of the remainder, 12 (67 spp.) probably cannot nodulate and 21 (40 spp.) have no or unconfirmed reports.

The whole situation in tribes Sophoreae and Swartzieae is confused by the fact that both have genera with and without the 50kb inversion of the chloroplast genome. Considering the genera that do not have this inversion, there are four small groups of Sophoreae, a group of Swartzioid genera and tribe Dipterygeae, all of which appear unable to nodulate. Separate from these, but also lacking the inversion, is the group of nodulated Swartzioid genera mentioned above. The one anomaly from the nodulation perspective is the inclusion of *Pickeringia* from tribe Thermopsideae, a problem discussed in Sprent (2007). Genera that have the 50kb inversion include most of Sophoreae, a tribe that is divided into several groups. Although the evidence is far

from complete, it cannot be excluded that all of these groups, except the one containing *Sweetia* and *Leutzelburgia*, contain only nodulating genera. *Sweetia* and *Leutzelburgia* are grouped with *Vatairia* and *Vatairiopsis*, two non-nodulating genera formerly in tribe Dalbergieae. Scattered among the groups of Sophoreae are some groups of non-nodulating Swartzioids (Pennington et al., 2005).

1.3.2 Nodulating papilionoids with primitive nodule structure

Five genera, (*Andira, Cyclolobium, Dahlstedtia, Poecilanthe,* and *Hymenolobium*), all with the 50kb inversion, are known to have bacteria retained within fixation threads (Fig. 1.2D), rather than released into symbiosomes (Fig. 1.2; Chapter 5). This feature is the norm in caesalpinioid legumes (see above) and has never been found in mimosoid legumes. It is also not known from nodules in tribe Swartzieae, generally considered to be basally branching within Papilionoideae. It is fair to say that the five genera listed above have been rather a headache for taxonomists, using a wide array of characteristics, but not including nodule structure. *Andira* and *Hymenolobium*, still formally placed in tribe Dalbergieae, are now included in a separate clade, close to the non-nodulating genera *Vatairia* and *Vatairiopsis* (Klitgaard & Lavin, 2005). The other three genera were earlier placed in tribe Millettieae, but *Cyclolobium* and *Poecilanthe* have recently been transferred to tribe Brongniartieae (Ross & Crisp, 2005), leaving *Dahlstedtia* in Millettieae. The present constitution of tribe Brongniartieae is given in Table 1.7. The large Australian component was formerly the *Templetonia* group of tribe Bossieaeeae (see section 1.3.5). Even within their new home, *Cyclolobium* and *Poecilanthe* are placed separate from the remainder of the tribe (Ross & Crisp, 2005). The only common features for the five genera with primitive nodule structure are that all are woody and all are found in South America, properties that are common to all but two of the nodulating caesalpinioid legumes (see section 1.1). Little is known of the rhizobia nodulating any of these genera or of other members of tribe Brongniartieae, with the exception of the Australian genera *Hovea* and *Templetonia*. The former was found to be nodulated only by bradyrhizobia in Southeast Australia (Lafay & Burdon, 1998) and both are nodulated by the fast-growing strain NGR 234 (Pueppke & Broughton, 1999).

Table 1.7 Nodulation in tribe Brongniartieae, genera as given in Ross & Crisp (2005)

Genus	Species	Nod.	Comment
Brongniartia Kunth.	~63	1	98% spp. in Mexico, none in Australia
Cristonia J.H. Ross	1	?	Ex *Templetonia*
Cyclolobium Benth	1	1	South America
Harpalyce Moçino & Sessé	24	2	Central America
Hovea R. Br. ex W.T. Aiton	37	8	Australia
Lamprolobium Benth.	2	1	Australia
Plagiocarpus Benth.	1	?	North Australia
Poecilanthe Benth	10–12	6	South America
Templetonia R. Br. ex W.T. Aiton.	10	2	Australia
Thinicola J.H. Ross	1	?	Ex *Templetonia*

In the overall phylogeny of legumes, as shown in Fig. 1 in Lewis et al. (2005), the tribe is placed near Sophoreae and far removed from the typical Australian tribes, discussed later.

1.3.3 Tribes with the 50kb inversion

All tribes discussed from this point on have the 50kb inversion. The first major branch, referred to as the Genistoid clade, is a rather heterogeneous group and includes some genera discussed earlier, i.e. those in tribe Brongniartieae, parts of Sophoreae, Swartzieae and anomalous members of old tribe Dalbergeae (the branch labelled 'various'). The remaining tribes included are Euchrestieae and Thermopsideae, which form a sub-clade with parts of Sophoreae and a group that includes Podalyrieae, Crotalarieae and Genisteae. On nodule characteristics, the last two fit well together, but the Podalyrieae have more in common with earlier tribes. They are so divided below.

Euchrestieae, Thermopsideae and Podalyrieae

Euchrestieae has only one genus, with four species found in Asia. It is likely that it will be included in a modified Sophoreae, possibly even included in genus *Sophora* (Ohashi, 2005). This is consistent with known nodulation characteristics. Thermopsideae are exclusively northern hemisphere and Podalyrieae exclusively South African, mainly from the Cape area. Their close relation thus seems a bit obscure. Table 1.8 lists their genera, but note that *Pickeringia* may be moved as discussed above. So far, genera in

Table 1.8 Genistoid tribes Thermopsideae and Podalyrieae

Tribe Genus	Species	Nod.
Thermopsideae		
Ammopiptanthus H.S. Cheng	1–2	1
Anagyris L.	2	2
Baptisia Vent.	15–17	5
Pickeringia Nutt.	1	1
Piptanthus Sweet	2	2
Thermopsis R. Br.	~23	8
Podalyrieae		
Amphithalea Eckl. & Zeyh.	42	3
Calpurnia E. Mey.	7	2
Cyclopia Vent	23	12
Liparia L.	20	5
Podalyria Willd	14	10
Stirtonanthus B.-E. van Wyk A.L. Schutte	3	?
Virgilia Poir.	2	2
Xiphotheca Eckl. & Zeyh.	9	2

Thermopsideae are only known to nodulate with α-rhizobia, but within that group, a range of fast- and slow-growing species. In Podalyrieae, five species of *Cyclopia* (Elliott et al., 2007b), three from *Podalyria* plus *Virgilia oroboides* (James & Sprent, unpublished data) can be nodulated by the β-rhizobium *Burkholderia tuberum*. In terms of nodule structure and morphology, both groups have indeterminate nodules, often branched and the infected tissue contains both infected and uninfected cells. Infection has not been widely studied, but in *Cyclopia* occurs through root hairs (Elliott et al., 2007b). Where information is available this is not true of tribes Crotalarieae and Genisteae (Sprent, 2007).

Crotalarieae and Genisteae

Genera in tribes Crotalarieae and Genisteae are given in Table 1.9. Both are likely to be revised. Whilst there appear to be similarities in nodule structure and possible infection mechanism, these two tribes have very different geographical ranges. Crotalarieae is largely African and this tribe will be considered first. Most species (about 510) of the largest genus, *Crotalaria*, are found in Africa, but there are significant numbers found in Asia and Australia (van Wyk, 2005). It was the first genus of legume where nodulation by non-classical rhizobia was reported. Sy et al. (2001) showed that a group of species of *Crotalaria* from Senegal could be split into two, depending on whether or not they could be nodulated by a methanol metabolising bacterium from the α-Proteobacteria, *Methylobacterium nodulans*. This division of species according to endophyte does not coincide with intraspecific groupings based on other characteristics (personal observations). Since then, similar results have been reported for species of *Lotononis* (Jafthe et al., 2002), a mainly South African genus, but extending into Mediterranean regions. Yates et al. (2007) showed that some, but not all species could be nodulated by a species of *Methylobacterium*, which in this case could not metabolise methanol. More details of these bacteria will be given in Chapter 4. *Aspalathus* is endemic to South Africa, with most species belonging to the Cape Floristic Region (CFR). Because of the importance of *A. linearis* for production of rooibos (red bush) tea, this species has been widely studied. However, the exact nature of its endophyte is still not clear. The genus as a whole nodulates with a variety of α-rhizobia (Deschodt & Strijdom, 1976), but a report of nodulation by *Burkholderia* (Moulin et al., 2001) has not been substantiated and Elliott et al. (2007b) found that several species could not be nodulated by *B. tuberum*, a species that nodulates several species of another CFR endemic, *Cyclopia* (tribe Podalyrieae). The genus *Lebeckia* as described by van Wyk (2005) has now been separated into three, *Calobota, Lebeckia* and *Wiborgiella* (Boatwright et al., 2008b). All are African, with most species in the CFR. The first two genera can be nodulated by α- and β- rhizobia (Phallane et al., 2008), but the endophyte of *Wiborgiella* spp. is not yet known. Nodules are indeterminate and can be extensively branched, a type of morphology described as crotalarioid by Corby (1988). Few detailed structural studies have been made, but those that have suggest that the infected tissue does not contain uninfected cells (summarised in Sprent, 2007). The recent study on *Lotononis angolensis* (Yates et al., 2007) clearly shows this and also that in this case nodule meristems may grow around the subtending root forming a type of nodule called

Table 1.9 Tribes Crotalarieae and Genisteae

Tribe Genus	Species	Nod.
Crotalarieae		
Aspalathus L.	278	70
Bolusia Benth.	5	1
Calobota Eckl. & Zeyh.[1]	16	6
Crotalaria L.[2]	~600	145
Lebeckia Thunb.[1]	14	11
Lotononis (DC) Eckl. & Zeyh.[1]	~150	62
Pearsonia Dümmer	13	6
Rafnia Thunb.	19	14
Robynsiophyton R. Wilczek	1	1
Rothia Pers.	2	2
Wiborgia Thunb.	10	4
Wiborgiella Boatwr. & B-E van Wyk[2]	9	1
Genisteae		
Adenocarpus DC.	~15	3
Anarthrophyllum Benth.	15	?
Argyrocytisus (Maire) Raynaud	1	?
Argyrolobium Eckl. & Zeyh.	~80	30
Calicotome Link	2–3	2
Cytisophyllum O. Lang	1	1
Cytisus Desf.[3]	~65	18
Dichilus DC.	5	3
Echinospartum (Spach) Rothm.	5	?
Erinacea Adans.	1	?
Genista L.	~90	18
Gonocytisus Spach.	3	?
Hesperolaburnum Maire	1	1
Laburnum Fabr.	2	2
Lembotropis Griseb.	2	1
Lupinus L.	220–230	65
Melolobium Eckl. & Zeyh.	15	9
Petteria C. Presl.	1	1
Podocytisus Boiss. & Heldr.	1	?
Polhillia C.H. Stirt.	7	?
Retama Raf.	4	3
Sellocharis Taub.	1	?
Spartium L.	1	1
Stauracanthus Link.	3	1
Ulex L	10–20	2

[1] See revision of *Lebeckia* in Boatwright et al. (2008b).
[2] Subject to revision.
[3] Includes *Chamaectyisus*.

lupinoid by Corby (1988) because it is commonly found in lupins (Fig. 1.1). Similar nodule structure is found in all eight species of section Listii (Ardley et al., 2008), but no other sections of the genus sampled so far (Sprent & van Wyk, unpublished data), which is interesting in view of the likelihood that section Listii may form the basis of a separate genus (B.E. van Wyk, personal communication). Clearly this tribe is of considerable interest for its nodulation characteristics.

Tribe Genisteae is also interesting from a nodulation point of view, but its characteristics are different from those of the Crotalarieae. Most of the genera are woody shrubs from Mediterranean regions, extending into Africa and sometimes into mountainous regions, especially in the New World. The largest genus, *Lupinus*, is complex, but has been widely studied because of its ability to grow on poor acid soils and because some of its species, such as *L. albus*, are important grain legumes. There are regular international symposia for the lupin fraternity, held in very different locations, such as Iceland, New Zealand and Australia. Genera in Genisteae are nodulated by a variety of α-rhizobia, with none yet known to use bacteria outside this group. Lupin nodules are formed following a type of epidermal infection and infection threads are rarely seen. In *Cytisus* (under its previous name *Chamaecytisus*), infection threads are transient and are not part of the infection mechanism (Vega-Hernández et al., 2001). A detailed study of *Genista tinctoria* also found that the infected tissue contained no uninfected cells (Kalita et al., 2006). More details of nodule structure and its significance will be given in Chapters 3 and 5. Species of *Lupinus* are amongst those that can grow at high altitudes and their isolation in some such locations has enabled them rapidly to develop new species (Hughes & Eastwood, 2006). Legumes in mountain habitats will be considered in Chapter 2. Because of their ability to grow on poor soils and exposed locations, many genistoid legumes, especially species of *Cytisus* and *Ulex*, have invaded areas such as Australia and New Zealand where they are generally regarded as noxious weeds. The genus *Polhillia* is native to the CFR and its nodulation status is not known.

Amorpheae

Tribe Amorpheae is placed close to the Dalbergioid clade in Lewis et al. (2005). Its genera are listed in Table 1.10. All are from North or Central America, with some extending into South America. Most have xerophytic characteristics and can grow in desert areas.

Table 1.10 Tribe Amorpheae

Genus	Species	Nod.
Amorpha L.	15	7
Apoplanesia C. Presl.	1	?
Dalea L.	~160	17
Errazurizia Phil.	4	?
Eysenhardtia Kunth.	~10	1
Marina Liebm.	38	1
Parryella Torr. & A. Gray	1	1
Psorothamnus Rydb.	9	4

At least two genera (*Amorpha* and *Dalea*) have indeterminate nodules (Corby, 1988), making them distinct from those in the Dalbergioid clade. They can apparently be nodulated by various α-rhizobia, but little detailed work has been carried out. However, it is now being realised that some of the native plants of North America are being threatened by agriculture and should be studied. Mártir et al. (2007) looked at *Dalea purpurea* (purple prairie clover) and found it to be nodulated by several species of *Rhizobium*.

1.3.4 The Dalbergioid clade

The Dalbergioid clade is unique in the Leguminosae in that one of the characteristics used to define it is nodule morphology (Lavin et al., 2001). Table 1.11 lists its genera, excluding the anomalous ones discussed in section 1.3.2. There are three major sub-clades, corresponding to the tribes that have been amalgamated to form the new clade, except that the Dalbergia sub-clade also includes former tribe Aeschynomeneae. The Adesmia and Pterocarpus groups are largely Central and South American. The Dalbergia group has members from either side of the Atlantic and some that are pantropical. All that have been described have aeschynomenoid nodules (Fig. 1.1), which are located in the axils of lateral or adventitious roots and whose infected tissue does not contain uninfected cells. Infection, where known, is via cracks in the epidermis where roots emerge. *Brya* and *Cranocarpus*, which Corby (1988) noted had aeschynomenoid nodules, were formerly placed in tribe Desmodieae, but are now in the Pterocarpus group. Two closely related genera, *Nissolia* and *Chaetocalyx* (Adesmia group), appear to have lost the ability to nodulate. Within genus *Pterocarpus*, Brazilian species appear unable to nodulate, although species from elsewhere in South America and in Africa can (Faria et al., 1989). The genus *Aeschynomene*, which is currently being revised, has a number of species that can form nodules on stems. These are always associated with adventitious root initials and are true stem nodules, in that they are plumbed into the vascular system of the stem. There have been several reports of stem nodules on other legumes (e.g. *Neptunia* spp., Mimoseae), but these have all been shown to be plumbed into adventitious roots (Subba-Rao et al., 1995). It is common for trees and lianas in rainforest to produce adventitious roots on their trunks and these can be profusely nodulated (Fig. 1.2D in Sprent, 2001). Stem nodules are normally formed in wet conditions, especially when the root system is flooded. *Discolobium pulchellum*, a species from the large Pantanal freshwater region in Brazil, is unusual in that stem nodules only form under water (Loureiro et al., 1994). Nodules in the Dalbergioid clade may be formed in association with various α-rhizobia, usually slow-growing forms. The report that *Machaerium* can be nodulated by *Burkholderia* (Moulin et al., 2001) is almost certainly the result of incorrect identification of plant roots. Rasolomampianina et al. (2005) isolated seven different genera of nodulating bacteria, both α- and β-, from *Dalbergia* species in Madagascar, but these remain to be fully authenticated.

1.3.5 The Mirbelioid clade

In Lewis et al. (2005), the Mirbelioid clade includes three tribes, Hypocalypteae, Mirbelieae and Bossiaeeae. The first of these has only one genus, with three species and is

Table 1.11 Genera defined in the dalbergioid clade of Lavin et al. (2001). Where structure has been studied, nodules are aeschynomenoid (Sprent, 2001). Some genera apparently have lost the ability to nodulate

New sub-clade		
Genus	Species	Nod.
Adesmia		
Adesmia DC.	240	7
Amicia Kunth.	7	3
Chaetocalyx DC.	13	0
Nissolia Jacq.	13	0
Poiretia Vent.	11	1
Zornia J.F. Gmel.	75	15
Dalbergia		
Aeschynomene L.[1]	180	49
Bryaspis P.A. Duvign.	2	1
Cyclocarpa Afzel. ex Bak.	1	1
Dalbergia L.f.	250	51
Diphysa Jacq.	15	1
Geissapsis Wright & Arn.	2	2
Humularia P.A. Duvign.	35	1
Kotschya Endl.	31	8
Machaerium Pers.	130	25
Ormocarpopsis R. Vig.	6	?
Ormocarpum P. Beauv.	18	3
Peltiera Labat & Dupuy[2]	2	?
Pictetia DC.	8	?
Smithia Aiton	20	12
Soemmeringia Mart.	1	?
Weberauerella Ulbr.	2	2
Zygocarpum P. Beauv.	6	?
Pterocarpus		
Arachis L.	69	16
Brya P. Browne	4	2
Cascaronia Griseb.	1	?
Centrolobium Mart. ex Benth.	7	3
Chapmannia Torr. & A. Gray	7	1
Cranocarpus Benth.	3	1
Discolobium Benth.	8	3
Etaballia Benth.	1	1
Fiebrigiella Harms	1	?
Fissicalyx Benth.	1	?
Geoffroea Jacq.	2	1
Grazielodendron H.C. Lima	1	0
Inocarpus J.R. Forst. & G. Forst.	3	1
Maraniona Hughes et al., 2004	1	?
Paramachaerium Ducke	5	1

(*Continued*)

Table 1.11 (*Continued*)

Genus	Species	Nod.
Platymiscium Vogel	19	6
Platypodium Vogel	2	1
Pterocarpus Jacq.[3]	40	18
Ramorinoa Speg.	1	?
Riedeliella Harms	3	1
Stylosanthes Sw.	25	21
Tipuana (Benth.) Benth.	1	1

[1] About 16 of these are able to form nodules on stems as well as roots.
[2] This Madagascan genus is thought to be extinct.
[3] Brazilian species appear unable to nodulate.

endemic to the Cape region of South Africa. Nothing is known of its nodule structure. Tribes Mirbelieae and Bossiaeeae (Table 1.12) are Australian, with some Mirbelieae extending into south Papua New Guinea. Their taxonomy has been extensively studied, but their nodulation and nodule characteristics are only now beginning to be understood. Nodules in both tribes are indeterminate, often branched. A wide variety of fast and slow-growing α-rhizobia can nodulate them, the exact species often depending on soil pH (Lafay & Burdon, 1998; Thrall et al., 2000). Nodule structure in *Aotus ericifolia* shows infected tissue to contain both infected and uninfected cells and infection threads are seen (Lawrie, 1981) This does not necessarily mean that there is a root hair infection pathway (Sprent, 2007). Most genera are found in dry, often arid areas, in soils of very low fertility, a point which will be discussed in Chapter 2. *Viminaria* is unusual in that it is found in seasonally flooded soils and has negatively geotropic roots (pneumatophores) as well as cluster roots (Walker et al., 1983). These tribes have recently (~5 Ma ago) diversified into arid areas (Chapters 2 and 3) and the characteristics that enable them to nodulate in environments that are generally regarded as unsuitable are urgently in need of study. Unfortunately, funds for studying nodulation in Australia (and in other countries) are targeted towards potential agricultural species. Members of these tribes may be toxic to grazing animals, with some species of *Gastrolobium*, for example, producing large quantities of fluoroacetate (Mead et al., 1985). Some populations of red kangaroos have co-evolved to cope with this.

1.3.6 The Millettioid clade

The Millettioid clade in Lewis et al. (2005) has three branches, first tribe Indigofereae, second Abreae + Millettieae, and third Desmodieae + Phaseoleae + Psoraleae. These branches will be considered in turn. Indigofereae has seven genera (Table 1.13), with the pantropical *Indigofera* being the third largest genus in Leguminosae. Although most species are African and Madagascan, considerable numbers are also found in Asia and Australia, with a few in the New World. Nodules are indeterminate and often branched, although *Indigofera linifolia* nodules when young appear desmodioid,

Table 1.12 Endemic Australian tribes

Tribe Genus	Species	Nod.
Bossiaeeae		
Aenictophyton A.T. Lee	1	?
Bossiaea Vent.	~60	16
Goodia Salisb.	2	2
Muelleranthus Hutch.	3	1
Platylobium Sm.	4	2
Ptychosema Benth.	2	?
Mirbelieae		
Almaleea Crisp & P.H. Weston.	5	?
Aotus Sm.	15–18	4
Callistachys Vent.	1	1
Chorizema Labill.	27	9
Daviesia Sm.	~135	20
Dillwynia Sm.	~40	12
Erichsenia Hemsl.	1	?
Euchilopsis F. Muell	1	1
Eutaxia R. Br. ex WT Alton	10	5
Gastrolobium R. Br.	109	24
Gompholobium Sm.	44	13
Isotropis Benth.	10	3
Jacksonia R. Br. ex Sm.	74	10
Latrobia Meisn.	6	1
Leptosema Benth.	13	1
Mirbelia Sm.	32	8
Otion Crisp & P.H. Weston	~8	?
Oxylobium Andrews	6	3
Phyllota (DC.) Benth.	11	3
Podolobium R. Br.	6	2
Pultenaea Sm.	104	27
Sphaerolobium Sm.	22	3
Stonesiella Crisp & P.H. Weston	1	?
Urodon Turcz.	4	?
Viminaria Sm.	1	1

Table 1.13 Tribe Indigofereae

Genus	Species	Nod.
Cyamopsis DC.	4	3
Indigastrum Jaub. & Spach.	~8	4
Indigofera L.	~700	200
Microcharis Benth.	36	3
Phylloxylon Baill.	7	?
Rhynchotropis Harms	2	?
Vaughania S. Moore	11	?

with lenticels, but when older become elongate, but retain the production of lenticels (H.S. Gehlot, personal communication). One species of *Indigastrum* is pan-tropical and genera *Phylloxylon* and *Vaughania* plus two species of *Microcharis* are from Madagascar, with the remaining species of all genera being African.

Abreae and Millettieae

Tribe Abreae has one pantropical genus, with seventeen species, four of which are known to nodulate. Nodules have been reported as desmodioid and (in other species) indeterminate, nodulating with slow-growing rhizobia (Sprent, 2001). In view of the fact that some phaseoloid genera are dimorphic for nodule morphology (see below), these data are consistent with placement of this genus near tribe Phaseoleae. Tribe Millettieae is complex, with two major groups being listed in Schrire (2005), with a much smaller third group (Table 1.14). The latter lacks the inverted repeat of the chloroplast genome and is included in the IRLC clade. (Fig. 1.5). The two main groups, referred to as the core and basal groups, span parts of the Phaseoleae. Somewhat depressingly, just over half the genera have not been examined for nodulation. However, all of those that have, from all three groups, possess indeterminate nodules, with the infected region containing both infected and uninfected cells. *Lonchocarpus muehlbergianus* lacks root hairs and is apparently infected between epidermal cells (Cordeiro et al., 1996). This feature may be of evolutionary significance (Sprent, 2007) as will be discussed in Chapter 3. As mentioned earlier, *Dahlstedtia* has primitive nodule structure. Where known, nodules are usually induced by slow-growing bacteria. In legume phylogenetic terms, understanding this largely tropical tribe is very important, and it is equally so for understanding nodule evolution. At present there is no reason on nodulation grounds to link any of the groups within the tribe to the remainder of the Millettioid clade, tribes Phaseoleae, Desmodieae and Psoraleae.

The Phaseoloid group; tribes Desmodieae, Phaseoleae and Psoraleae

Apart from some members of the temperate tribe Loteae (see section 1.3.7), tribes Desmodieae, Phaseoleae and Psoraleae (Table 1.15) are the only ones to have determinate (desmodioid) nodules (Figs. 1.1 and 1.2). There are occasional reports of genera with dimorphic nodules, for example in *Kennedia* and *Erythrina*. Also, although young nodules may be desmodioid, occasionally they may become lobed, or even branched when older (Sprent, 2001) All those tested from these tribes export ureides rather than amides as the products of nitrogen fixation (Sprent, 2001; Kanu et al., 2008, chapter 5). In current thinking, tribes Desmodieae and Psoraleae are nested within tribe Phaseoleae (Schrire, 2005), a fact entirely consistent with nodulation characteristics. However, there are still many genera that have not been sampled for either molecular or nodulation characteristics (42 out of 128 for the latter). Unlike many other legume tribes, there are no confirmed cases of phaseoloid legumes being unable to nodulate.

Two sub-tribes of Phaseoleae, Diocleinae (13 genera) and Ophrestiinae (3 genera), are separated from the rest of the group on molecular characteristics, being placed close to the core Millettieae. However, where known, their nodulation characteristics place them clearly in Phaseoleae (Sprent, 2001; Pueppke & Broughton, 1999). With some

Table 1.14 Tribe Millettieae. The three informal groups of Schrire (2005), core (C), basal (B) and IRLC groups are indicated

Genus	Species	Nod.	Group
Afgekia Craib	3	?	IRLC
Aganope Miq.	~7	1	B
Antheroporum Gagnep.	~4	?	IRLC?
Apurimacea Harms	~2	?	C
Austrosteenisia Geesink	4	?	C
Behaimia Griseb.	1	?	C
Bergeronia M. Micheli	1	1	C
Burkilliodendron (Ridl.) Sastry	1	?	B
Callerya Endl.	~20	2	IRLC
Chadsia Bojer	9	1	C
Craibia Harms & Dunn	10	1	B
Craspedolobium Harms	1	?	B
Dahlstedtia Malme.	2	1	C
Dalbergiella Baker f.	3	1	B
Deguelia Aubl.	~17	5	C
Derris Lour.	55–60	2	C
Dewevrea Micheli	1–2	1	B
Disynstemon R. Vig.	1	?	B?
Endosamara Geesink	1–2	?	IRLC
Fordia Hemsl.	18	?	B
Hesperothamnus Brandegee	5	?	C
Kunstleria Prain	8	?	B
Leptoderris Dunn.	~20	3	B?
Lonchocarpus Kunth.	~120	13	C
Margaritilobium Harms	1	?	C
Millettia Wight & Arn.	~150	16	C
Muellera L.f.	2	?	C
Mundulea (DC.) Benth.	12	1	C
Ostryocarpus Hook f.	1–2	?	B
Paraderris (Miq.) Geesink	~13	?	C
Paratephrosia Domin.	1	?	C
Philenoptera Fenzl. ex A. Rich.	12	4	C
Piscidia L.	~7	2	C
Platycyamus Benth.	2	1	B
Platysepalum Welw. ex Baker	7–8	?	B?
Pongamiopsis R. Vig.	3	?	C
Ptycholobium Harms	3	3	C
Pyranthus Du Puy & Labat.	6	?	C
Requiena DC.	3	2	C
Sarcodum Lour.	~3	?	IRLC
Schlefflerodendron Harms	4	?	B
Sylvichadsia Labat & Du Puy	4	?	B?
Tephrosia Pers.	~350	83	C
Wisteria Nutt.	5–6	6	IRLC
Xeroderris Roberty	1	1	B

Table 1.15 Tribes with determinate nodules and, where tested, exporting the ureides allantoin and allantoic acid as products of nitrogen fixation

Tribe Genus	Species	Nod.
Desmodieae		
Ackschlindlium H. Ohasi	1	?
Alysicarpus Desv.	25–30	14
Aphyllodium (DC) Gagnep.	7	1
Arthroclianthus Baill.	~30	?
Campylotropis Bunge	~37	2
Christia Moench	~10	2
Codariocalyx Hassk.	3	2
Dendrolobium (Wright & Arne)	18	3
Desmodiastrum (Prain) A. Pramanik & K. Thothathri	4	?
Desmodium Desv.	~275	74
Droogmansia De Wild	~5	2
Eleiotis DC.	2	?
Hanslia Schindl.	2	?
Hegnera Schindl.	1	?
Hylodesmum H. Ohashi & R.R. Mill.	14	5
Kummerowia Schlindl.	2	2
Leptodesmia (Benth.) Benth.	5	?
Lespedeza Michx.	~35	31
Mecopus Benn.	1	?
Melliniella Harms.	1	?
Monoarthrocarpus Merr.	1	?
Nephrodesmus Schindl.	6	?
Ougeinia Benth.	1	1
Ohwia H. Ohashi.	2	1
Phyllodium Desv.	8	2
Pseudarthria Wight & Arn.	3–4	2
Pycnospora R. Br. ex Wight & Arn.	1	1
Tadehagi H. Ohashi.	~6	1
Trifidacanthus Merr.	1	?
Uraria Desv.	~20	7
Phaseoleae		
Adenodolichos Harms.	15–20	1
Alistilus N.E. Br.	3	1
Amphicarpaea Elliot ex Nutt.	4–5	2
Apios Fabr.	~7	2
Austrodolichos Verdc.	1	?
Barbieria DC.	1	0?
Bolusafra Kuntze.	1	1
Butea Roxb. ex Willd.	2	1?
Cajanus DC.	34	7
Calopogonium Desv.	5–6	2
Camptosema Hook. & Arn.	10	3
Canavalia DC.	~60	7
Carrissoa Baker f.	1	?

Table 1.15 (*Continued*)

Tribe Genus	Species	Nod.
Phaseoleae		
Centrosema (DC.) Benth.	~36	14
Chrysoscias E. Mey	3–4	?
Cleobulia Mart. ex Benth.	3–5	1
Clitoria L.	~62	12
Clitoriopsis R. Wilczek.	1	?
Cochlianthus Benth.	2	?
Collaea DC.	7	1
Cologania Kunth.	~12	2
Cratylia Mart. ex Benth.	~7	3
Cruddasia Prain	~2	?
Cymbosema Benth.	1	?
Decorsea R. Vig.	6	1
Dioclea Kunth.	~40	9
Diphyllarium Gagnep.	1	?
Dipogon Liebm.	1	1
Dolichopsis Hassl.	1	1
Dolichos L.	~60	13
Dumasia DC.	~10	2
Dunbaria Wight & Arn.	20	4
Dysolobium (Benth.) Prain.	4	1
Eminia Taub.	~4	1
Eriosema (DC.) Rchb.	~150	29
Erythrina L.	~120	40
Flemingia Roxb. ex W.T. Aiton.	30–35	8
Galactia P. Browne	55–60	10
Glycine Willd.	19	17
Hardenbergia Benth.	3	2
Herpyza Sauvalle	1	?
Kennedia Vent.	~15	13
Lablab Adans.	1	1
Lackeya R.H. Fortunata, L.P. de Queiroz & G.P. Lewis.	1	?
Luzonia Elmer	1	?
Macropsychanthus Harms ex K. Schum. & Lauterb.	~2	?
Macroptilium (Benth.) Urb.	~17	7
Macrotyloma (Wight & Arn.) Verdc.	24	11
Mastersia Benth.	2	1
Meizotropis J. Voigt	2	?
Mucuna Adans.	~105	17
Mysanthus G.P. Lewis & A. Delgado	1	?
Neocollettia Hemsl.	1	?
Neonotonia Lackey	2	1
Neorautanenia Schinz.	5	3
Neorudolphia Britton	1	1
Nesphostylis Verdc.	4	?
Nogra Merr.	~3	?

(*Continued*)

Table 1.15 (*Continued*)

Tribe Genus	Species	Nod.
Phaseoleae		
Ophrestia H.M.J. Forbes.	~16	3
Oryxis A. Delgado & G.P. Lewis	1	?
Otoptera DC.	2	1
Oxyrhynchus Brandegee	4	1
Pachyrhizus Rich. ex DC.	5	4
Paracalyx Ali	6	?
Periandra Mart. ex Benth.	6	2
Phaseolus L.	60–65	11
Phylacium Benn.	2	?
Physostigma Balf.	~4	?
Pseudeminia Verdc.	4	1
Pseudoeriosema Hauman	~4	?
Pseudovigna (Harms) Verdc.	2	1
Psophocarpus DC.	~10	5
Pueraria DC.	~18	4
Ramirezella Rose.	7	1
Rhodopsis Urb.	2	?
Rhynchosia Lour.	~230	61
Shuteria Wight & Arn.	4–5	2
Sinodolichos Verdc.	2	?
Spathionema Taub.	1	?
Spatholobus Hassk.	29	2
Sphenostylis E. Mey.	7	4
Strongylodon Vogel.	12	3
Strophostyles Elliot	3	3
Teramnus P. Browne	9	4
Teyleria Backer	3	1
Vandasina Rauschert	1	1
Vatovaea Chiov.	1	?
Vigna Savi	~104	49
Wajira Thulin	5	1
Psoraleae		
Bituminaria Heist. ex Fabr.	2	2
Cullen Medik.	~34	11
Hoita Rydb.	3	2
Orbexilum Raf.	8	3
Otholobium C.H. Stirt.	61	10
Pediomelum Rydb.	21	3
Psoralea L.	~50	19
Psoralidium Rydb.	3	2
Rupertia J.W. Grimes	3	?

notable exceptions, such as tree species of *Erythrina*, most of the species in this group of tribes are small shrubs or herbaceous annuals and perennials. Apart from some species of *Lupinus* (tribe Genisteae), *Arachis* (peanut, groundnut, tribe Dalbergieae), *Vicia* and *Pisum* (tribe Fabeae), tribe Phaseoleae houses the world's most important grain legumes, as well as many forage, browse and tuber species These are described in many books, including Allen & Allen (1981) and Anon (1979), and some will be discussed further in Chapter 5. A few species, such as soybean (*Glycine max*) and dry bean (*Phaseolus vulgaris*), are industrial crops, although the latter is also extremely important for subsistence farmers in many developing countries, and thus their symbiosis with rhizobia has been extensively studied. This is particularly true for soybean. In the US, unlike Brazil, breeders have generally selected potentially high-yielding cultivars on fertilized plots and thus have unwittingly selected against nitrogen fixation. Denison and co-workers have been studying ways in which soybean plants might sanction against ineffective rhizobia and ensure that they only nodulate with effective strains. In their most recent study (Kiers et al., 2007), they have looked at a range of historic and modern cultivars and concluded that the latter were less able to sanction against inefficient rhizobia.

The ability to export ureides has been linked to the tropical and sub-tropical habitats of this group of legumes, for various reasons including their low solubility (Sprent, 1980). It would be interesting to know whether species occurring naturally in cooler areas – such as in the three genera *Strophostyles* (Phaseoleae), *Pediomelum* and *Rupertia* (Psoraleae) that are found in Southern Canada – export ureides. Because of their determinate nature, desmodioid nodules have a limited life span (usually a few weeks) and cannot regrow after environmental stress, unlike nodules with an apical meristem, which may be perennial. This again has been linked to living in warmer regions. The main environmental threat is drought and this may lead to nodule loss.

As might be expected of such a large group of genera, nodulation can be induced by a wide variety of bacteria. These include many genera of α-rhizobia, both fast- and slow-growing. The first reports of nodulation by β-rhizobia are now appearing. In their study of nodulation in *Cyclopia* (Podalyrieae), Elliot et al. (2007b) found that *Burkholderia tuberum* could effectively nodulate the promiscuous host plant *Macroptilium purpureum* (Desmodieae). More recently Garau et al. (2009) isolated a new species of *Burkholderia* from *Rhynchosia ferulifolia*, a phaseoloid species endemic to the Cape region of South Africa. This bacterium did not nodulate other species of *Rhynchosia* tested. Pueppke and Broughton (1999) tested a vast number of legumes for ability to nodulate with the wide host range bacterium NGR 234, isolated from Papua New Guinea, including five species of *Rhynchosia*. Three of these, all from either Africa or Asia, formed effective nodules, but the other two, from Central and South America, did not nodulate at all with this strain. Species of this very large genus appear to show quite a high level of specificity with widely differing bacteria. This contrasts, for example, with *Phaseolus vulgaris*, which nodulates with a wide range of rhizobia, but as yet none outside the major α-rhizobia.

1.3.7 The Robinioid clade

In Lewis et al. (2005) the Robinioid clade has three tribes, Loteae, Sesbanieae and Robinieae (Tables 1.1, 1.16), forming an interesting group from a nodulation point of

Table 1.16 Tribes Sesbanieae, Robineae and Loteae. The latter now includes Coronilleae, but the genera in these former tribes have been kept separate here, because of their different nodule morphologies

Tribe Genus	Genus	Nod.
Sesbanieae		
Sesbania Adans.	60	38
Robineae		
Coursetia DC.	~35	2
Genistidium I.M. Johnst.	1	?
Gliricidia Kunth.	5	1
Hebestigma Urb.	1	1
Lennea Klotzsch	3	?
Olneya A. Gray	1	1
Peteria A. Gray	4	?
Poissonia Baill.	4–5	?
Poitea Vent.	12	1
Robinia L.	4	2
Sphinctospermum Rose	1	?
Loteae Nodules determinate		
Acmispon Rafin.	8	2
Anthyllis L.	22	5
Cytisopsis Jaub. & Spach	2	?
Dorycnium Miller	8	4
Dorycnopsis Boiss.	2	?
Hosackia Benth. ex Lindl.	11	3
Hymenocarpos Savi.	1	1
Keberita Kramina & D.D. Sokoloff	1	1
Lotus L.	~125	53
Ottleya D.D. Sokoloff	11	2
Podolotus Benth.	1	1
Pseudolotus Rech. f.	1	?
Syrmatium Vogel	14	4
Tetragonolobus Scop.[1]	6	3
Tripodion Medik.	1	1
Former Coronilleae, indeterminate nodules, where known		
Antopetitia A. Rich.	1	1
Coronilla L.	9	4
Hammatolobium Fenzl	2	?
Hippocrepis L	34	6
Ornithopus L.	~5	5
Scorpiurus L.	2	2
Securigera DC.	13	4

[1] May be included in *Lotus* (Sokoloff & Lock, 2005).

view. The genus *Sesbania* has been taken out of tribe Robinieae and put in a tribe of its own (Lavin & Schrire, 2005). Some species are able to form nodules located on stems, but plumbed into adventitious root initials. *S. rostrata* has its own nodulating genus, *Azorhizobium caulinodans*, the only genus of the α-rhizobia so far shown to fix and assimilate nitrogen ex planta (Chapter 5). Stem nodules superficially appear aeschynomenoid, and have a crack infection, but later form infection threads and are structurally unlike aeschynomenoid nodules. Under certain conditions they become indeterminate and nodules on roots (these can be induced by rhizobia other than *A. caulinodans*) are infected via root hairs. These features are discussed in more detail in Chapter 5.

Tribe Robinieae (Table 1.16) is confined to the Americas and the Caribbean. Some species of *Coursetia* have been transferred to *Poissonia* and *Sphinctospermum* is now placed here rather than in Millettieae. The most widely studied species is *Robinia pseudoacacia*, which is widely grown as an ornamental, but which suckers badly and can become very invasive, for example in parts of Europe. *Gliricidia sepium* is widely used in agroforestry in Africa and elsewhere. It and other species in this tribe can nodulate with a wide variety of bacteria, with varying degrees of effectiveness (Bala & Giller, 2001). Nodules are generally indeterminate with no known unusual features.

Molecular and morphological data have now firmly placed former tribe Coronilleae in tribe Loteae, which is a pity from a nodulating point of view since genera in it have indeterminate and in the former Loteae determinate nodules (Corby, 1988; Sprent, 2001). In the revised Loteae, there are two main groups and these do not correspond to the former tribes (Sokoloff & Lock, 2005). The current tribe Loteae is thus an anomaly in its nodule characteristics. However, although some are determinate, they do not export ureides, as in the determinate nodules of the Phaseoloid group (see section 1.3.6). Some, such as *Lotus uliginosus*, can be found in the far north of Europe, where indeterminate nodules are the norm. These aspects will be discussed again in Chapters 2 and 5. The overall distribution of the tribe is north temperate, but extending down to South America and some species of *Lotus* are also found in Australia. *L. japonicus* is one of the 'model' legumes under intensive study (Chapter 3). Apart from this species, little is known of the rhizobia nodulating members of tribe Loteae, except that they are usually fast growing.

1.3.8 The inverted repeat lacking clade (IRLC)

The final group of tribes (together with some anomalous parts of other tribes) form the IRLC clade (Fig. 1.5), whose members have lost an inverted duplicated insertion in the chloroplast genome. This is a major genetic change and if it has only happened once, then those genera that have it should be segregated from those that do not. This would also apply to the third group of the Milletteae, discussed above. The tribes within it are Galegeae, Hedysareae, Cicereae, Trifoleae and Fabeae. Almost all genera are temperate or boreal, and all have indeterminate nodules, usually nodulated by fast growing rhizobia, with large variations in degrees of specificity (Chapters 4 and 5). There are no known genera that lack the ability to nodulate, suggesting that nodulation is particularly important in these geographical regions (Chapter 2). The genera are

Table 1.17 Tribes in the IRLC clade

Tribe Genus	Species	Nod.
Cicereae		
Cicer L.	43	3
Fabeae		
Lathyrus L.	~160	47
Lens Mill.	4–6	4
Pisum L.	2–3	1
Vavilovia Al. Fred	1	1
Vicia L.	~160	59
Galegeae		
Astragalus L.	2300+	~119
Barnebyella D. Podlech.	1	?
Biserrula L.	1	1
Carmichaelia R. Br.	23	13
Chesnya Lindl. ex Endl.	~30	1
Clianthus Sol. ex Lindl.	2	2
Colutea L.	~28	6
Eremosparton Fisch. & C. Mey	3	1
Erophaca Bioss.	1	1
Galega L.	6	3
Glycyrrhiza L	~20	8
Gueldenstaedtia Fisch.	~10	1
Lessertia DC.	~50	27
Montigena Heenan	1	1
Ophiocarpus (Bunge) Ikonn.	1	?
Oreophysa (Bunge ex Boiss.) Bornm.	1	?
Oxytropis DC.	300–400	22
Smirnowia Bunge	1	1
Sphaerophysa DC.	2	1
Spongiocarpella Yakovlev & N. Ulziykh	~7	?
Sutherlandia R. Br. ex W.T. Aiton	2	1
Swainsona Salisb.	24	21
Tibetia (Ali) Tsui.	4	1
Hedysareae		
Alhagi Gagneb.	~3	2
Calophaca Fisch. ex DC.	5–8	1
Caragana Fabr.	70–80	21
Corethrodendron Fisch. & Basin	4	2
Ebenus L.	~20	1
Eversmannia Bunge	4	?
Halimodendron Fisch. ex DC.	1	1
Hedysarum L.	140–180	11
Onobrychis Mill.	~130	15
Sartoria Boiss. & Heldr.	1	?
Sulla Medik	7	6
Taverniera DC.	15	2

Table 1.17 (*Continued*)

Tribe Genus	Species	Nod.
Trifolieae		
Medicago L.	83	43
Melilotus Mill.	~20	16
Ononis L.	~75	20
Parochetus Buch.-Ham. ex D. Don	2	1
Trifolium L.	~250	131
Trigonella L.	~55	23

listed in Table 1.17. There have been significant recent changes. The New Zealand tribe Carmichaelieae (*Carmichaelia, Montigena*) is incorporated into Galegeae. Some species of *Clianthus* (New Zealand) have been transferred to *Swainsona* (Australian). *Astragalus*, currently the largest genus in Leguminosae, has had some species transferred to new genera (*Erophaca*, *Ophiocarpus*) with more likely to follow in other new genera. The genus may eventually form the basis of a separate tribe. *Lessertia* and *Sutherlandia* are unusual in this group of tribes in being African endemics. Some species of *Oxytropis* grow within the Arctic circle. Many genera, including *Gueldenstaedtia*, *Chesnya* and *Tibetia* (Galegeae) have species that can be found high in the Himalayas. *Halimodendron* (Hedysareae) is a salt-tolerant plant of steppes. Many species of all tribes are important forage plants. *Cicer arietinum*, *Lens culinaris*, *Pisum sativum* and *Vicia faba* have a long history of agricultural use as major grain species and are often known collectively as cool season grain legumes, because they grow in Mediterranean areas with cool wet winters and warm, dry summers. Although being the largest fraction of Papilionoideae (and hence Leguminosae), this group presents few taxonomic challenges from a nodulation point of view: they are generally nodulated by α-rhizobia.

Chapter 2

Global Distribution of Legumes

Legumes are found in all areas of the world except for open seas; in other words, wherever other angiosperm families are found. However, the proportion of legumes versus other families varies greatly. There are also large variations in the proportions of legumes that are nodulated or not in a particular environment and, where they are nodulated, the efficiency with which their nodules fix nitrogen. What are the properties of legumes generally that enable them to colonise particular environments so successfully, and why, in some environments, is the added benefit of nitrogen fixation an advantage? This chapter will discuss these questions for the major geographical regions of the world, in the general context of the four biomes discussed in Schrire et al. (2005), but with some deviations. These biomes are outlined in Table 2.1. Many areas have intermediate features; for example, the Cerrado region of Brazil has both seasonally dry tropical forest (SDTF) and savanna characteristics. Some areas, such as the Miombo woodlands of Africa, are not included, as they have been covered elsewhere (Högberg & Alexander, 1995; see also Sprent, 2001). Almost every book on tropical ecology defines savannas in a slightly different way. In this chapter particular examples will be given, including soil and climate features where these appear in part to define the functional groups of flora present. Because of current concerns, a section on invasive legumes will also be included. The biogeographical sections start with deserts and proceed via increasing moisture to rain forests, with the temperate areas at the end. As there are major problems in estimation of nitrogen fixation at the field scale in natural ecosystems, there is no systematic attempt to do this here.

2.1 Deserts

Although nodulated legumes are known to grow in deserts, there has been no published systematic study of their ability to nodulate and fix nitrogen there. One of the most drought and saline tolerant genera is *Prosopis* (Mimosoideae). Several species are native to Chile and can be grown in extremely dry and saline conditions. They may absorb water from mist through their leaves and some can bring up water from deep in the

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Table 2.1 Major biomes. After Schrire et al. (2005)

Biome	Characteristics
Succulent	Also known as seasonal dry tropical forests (SDTF). Semi-arid areas where plants are not tolerant of fire and which are grass poor. Succulents are common. Includes deserts
Grass	Succulent poor, but grass rich. Tolerant of fire. Includes some SDTF and all savannas
Rainforest	Confined to the equatorial tropics
Temperate	The largest of the biomes, found in both hemispheres, but often with distinct legume genera

soil (hydraulic lift). In either case, water may be transported down or up the plant and exuded from roots, thus supporting rhizosphere processes. *P. tamarugo* has been used to re-afforest the extreme salt desert in the Tamarugal Pampa area of Chile, so that it can now support livestock (Anon, 1979). Other species of the genus are native to sub-saharan Africa and the Southwest of the United States (Plate 2.1). Because of their tolerance of extreme conditions, species of *Prosopis* are being introduced into other dry areas, where they may be nodulated by a wide variety of fast-growing rhizobia, although not always effectively (Bala & Giller, 2001; Iglesias et al., 2007). In very saline conditions, *Prosopis alba* may be nodulated by *Mesorhizobium chacoense* (Graham, 2008). Whereas most legumes grow better in extreme conditions when grown on combined rather than fixed nitrogen, *P. articulata, P. pallida* and *P. tamarugo* can fix nitrogen in saline solution at the strength of sea water (Felker et al., 1981). Felker (2008) has published a comprehensive review of the potential for development of *Prosopis* spp., noting the wealth of genetic variation and the fact that its small genome make it suitable for genetic manipulation. It has a very wide range of uses, ranging from firewood to flour for cooking. Another genus that has species very tolerant of drought and salinity is *Acacia* (sl). Here, the strategies vary between sub-genera. *Acacia* and *Aculeiferum* usually shed all or part of their leaf biomass under stress (Plate 2.2), whereas the largely Australian *Phyllodineae* retains its phyllodes, and can be drought/salinity tolerant (Plate 2.3). In the Negev in Israel, *Acacia tortilis, A. raddiana* and *A. pachyceras* are the only trees present in most of the desert and are considered to be keynote species because of their effects on the flora underneath and around them (Zuzana & Ward, 2002). However, nitrogen fixation was not measured, although these species are known to be able to nodulate. Some of the positive effects may have been due to their access to ground water (as for *Prosopis* spp.), although there are also negative effects resulting from bringing up salts with the water. In the Taklamakan desert in central Asia, the ground water table is relatively shallow (2–16 m), enabling plants to grow there even though precipitation is below 50 mm annually. This water contains high levels of nitrate and yet the herbaceous legume *Alhagi sparsifolia* fixes over 50% of the nitrogen it needs (Arndt et al., 2004). This calls into question the perceived wisdom that combined nitrogen, especially nitrate, inhibits nitrogen fixation. Overall, it seems that most perennial woody legumes in deserts need access, directly or indirectly, to ground water. It must be remembered that salinity is often accompanied by waterlogging, which imposes stresses different from those of drought. Further, salinity is not always caused by sodium chloride, and sodic soils

with a high pH also impose their own constraints. However there are some species, for example the mimosoid *Leucaena leucocephala*, that grow well in these conditions (Plate 2.4).

There are some herbaceous annual legumes such as species of *Kennedia* (tribe Phaseoleae) that germinate, nodulate and grow rapidly after rain events in desert areas. Other, perennial herbs may grow the wet season and store water and nutrients in subterranean tubers in the dry season. Several species of *Vigna* do this, mainly in Africa and Asia, with other genera also occurring there and in the New World (Anon, 1979; see also Chapter 6 of the present book). Tubers of these species rival legume seeds in nutrient quality, but most of them are only used at a local scale and have not been developed for agriculture. Possibly the largest tubers are produced by *Tylosema esculentum*, which also produces edible seed, both parts being used by bushmen in the Kalahari. Unfortunately this caesalpinioid species does not nodulate. There are a number of caesalpinioid trees that are very drought tolerant and of economic use, but which do not nodulate. Examples are *Parkinsonia aculeata* and *Cordeauxia edulis*.

The Thar Desert of Western Rajastan in India supports a large number of legumes, some perennial, some annual and some invasive species from outside the region. A programme of research on this interesting system has recently been started and is already producing significant new data (H.S. Gehlot, personal communication). Thirty-three nodulated legumes, including some from each subfamily, have so far been recorded. These include six species of *Indigofera*, seven of *Tephrosia*, two of *Crotalaria* and one of *Rhynchosia* as well as an endemic *Mimosa*. Some of these genera have species that are known to nodulate with β-rhizobia and unusual α-rhizobia (Chapter 4). With global change, such studies are likely to become increasingly important.

Large areas of northern Eurasia are deserts, coupled with very low temperatures. Many of these are also at high altitude and will be considered in section 2.5.2.

2.2 Savannas

Savannas will be considered mainly on a continental basis as there are major differences in the role of nodulated legumes in these areas. In geological terms they are relatively recent, developing at the time when C_4 grasses first evolved, about 10 million years ago. Fires occur at varying intervals and are an important part of the functioning ecosystems. Although Houlton et al. (2008) suggest that in phosphorus-limited tropical savannas nodulated legumes can afford to use nitrogen to synthesise phosphorus-acquisition systems, this may not always be the case, since nodules are not always effective in some regions.

2.2.1 African savannas

Scholes and Walker (1993) give a map of Africa where almost half the continent has some savanna, but designate 'core' savanna areas as those where over 80% of the vegetation is savanna, the rest having 20% to 80% of savanna, with transition into forests and arid shrublands. Even in the core areas, there is great variation, both in soil

fertility and rainfall, the latter ranging from 350 to 1800 mm per annum. African soils fall into two major categories, the old (dating from the breakup of Gondwana) and the new, more recent soils. In general the old soils are less fertile than the new, but the latter may be complicated by the buildup of salts, such as in many regions of Kenya. The state of knowledge of the ecosystems in different areas varies greatly, so this section is based on selected references, to illustrate both the diversity of the legume flora and its contribution to the nitrogen economy of the ecosystem.

The work of Scholes and Walker (1993) in the Nylsvley area of southeast South Africa illustrates the complexity of the ecosystems, including the confounding effects of the fauna (including people). They recognise two types of savanna. One, on the less fertile sites, is dominated by non-nodulating trees, in particular the legume *Burkea africana*, an evergreen, large-leaved species. However, although savannas are generally thought of as trees and grasses, there may be a significant number of legumes in the ground flora. In the case of the *Burkea* savanna, these included ten species with demonstrated or suspected nitrogen fixing activity (including *Cassia biensis*, which is a synonym for *Chamaecrista biensis*). In the drier, more nutrient rich areas, nodulated *Acacia tortilis* is dominant, as it is in many parts of Africa (Plate 2.5). The extent and importance of nodulation in acacias in Africa is very variable. Frequently species that are known to be able to nodulate do not do so under certain conditions. One recent study in South Africa (Cramer et al., 2007) used four species of *Acacia*, including *A. tortilis*, grown on soils with some residual nitrogen, with and without a grass component. In the absence of grass, the soil nitrogen was sufficient to depress nodulation, but in the presence of grass, there was good nodulation and nitrogen fixation, as a result of the grass using the soil nitrogen and 'forcing' the legume to provide its own. A similar situation has been found in northern temperate grass-legume pastures (Carlsson, 2005), suggesting that it may be a general phenomenon. In natural ecosystems, legumes seldom grow in monoculture. Another feature of some African acacias is that their root systems penetrate great depths, especially in some of the sandier savanna areas, such as parts of East Africa and Senegal and deserts of the Kalahari and Namibia. Data from leaves of five species grown in Zimbabwe, where nitrogen fixation was estimated by the natural abundance $\delta^{15}N$ method (Boddey et al., 2000), showed wide variation between species (data of J.M. Sutherland, cited in Barnes et al., 1997). In particular there was no evidence of fixation in *A. erioloba*, and no nodules were found on its plants. Indeed there have been reports that this species cannot nodulate. However, this is not true, but it does have very long roots that can access mineral nitrogen in ground water and thus may not always need to nodulate. It is still of use in the overall nitrogen economy of the system as it makes available nitrogen that other plants cannot access. As mentioned in Chapter 1, some species of African and South American acacias appear to have lost the ability to nodulate. Those that can often use a wide variety of rhizobia (Chapter 4), with a wide range of efficiency of nitrogen fixation. The savanna areas where these species grow generally have very low and erratic rainfall and are nutrient poor. They do, however, have plenty of light for photosynthesis, and it has been argued that if water is the major factor limiting growth, nodulation and nitrogen fixation are of lesser importance (Sprent, 2007). Savannas in other areas, such as parts of South America, may be different. In more humid African savannas, such as in parts of Tanzania, nodulated acacias may significantly increase soil nitrogen (Cech et al., 2008).

2.2.2 Neotropical savannas

The largest neotropical savannas are in the Llanos of Venezuela and Colombia and the Cerrados of central Brazil. Fortunately the latter have been extensively studied over the last decades, together with their adjacent seasonally dry tropical forests (SDTF). This section will thus concentrate on Brazil and much of the information is contained in a volume edited by Pennington et al. (2006). Both the Cerrados and SDTF are being extensively converted to agricultural use, including production of soybeans, grasslands for cattle and, more recently sugar cane for bioethanol production. The Cerrado biome alone covers 2 million km^2 of central Brazil and is ranked as one of the 25 global hot spots for biodiversity (Myers et al., 2000). The soils are dystrophic, like some of the older soils of Africa, being acid, freely draining with high levels of aluminum and low levels of available magnesium and calcium. The vegetation varies from grassland with a sparse covering of trees, to almost enclosed woodland (Plate 2.6). Fire is frequent and much of the woody flora is well adapted to this, for example, by producing xylopodia from which new shoots are produced after fire (Plate 2.7). The woody vegetation has been most extensively studied and in all areas the legumes come out highest in terms of number of species, many of which are endemic (Ratter et al., 2006). Of these, *Mimosa* is the largest genus and appears to be uniformly nodulated (Elliott et al., 2007a; E.K. James et al., unpublished data). However, the lower shrubs and herbaceous angiosperm flora also have a high proportion of legumes, with *Chamaecrista* being among the most numerous and also uniformly nodulated (Sprent et al., 1996). Brazil is a centre of diversity for both these large genera. The endophytes of *Chamaecrista* in Brazil have not been studied, but those of *Mimosa* in Brazil are almost exclusively β-rhizobia (James et al., unpublished data; see also Chapter 4). All the available evidence suggests that nodules are effective. Trying to estimate how much nitrogen is fixed in the field is fraught with difficulties, with the $\delta^{15}N$ methods being the only option. In woody ecosystems, this has major problems (Boddey et al., 2000), but even so, Sprent et al. (1996) calculated that *Chamaecrista* nodules and those of various herbaceous legumes fixed significant amounts of nitrogen. This was supported by work on *Mimosa* nodules from the field that were shown to have functional nitrogenase protein, using immunolabelling for the *nifH* protein (E.K. James, personal communication). Thus the situation contrasts with that in African savannas, where nitrogen fixation appears to be more variable. A reason for this may be that Brazil has one of the moister savanna regions, with rainfall of 800 to 2000 mm. Although there is a pronounced dry season, drought is less of a problem than in many African savannas. It is also noteworthy that there are relatively few non-nodulated legumes found in the Cerrados.

2.2.3 Australian savannas

It has been estimated that nearly a quarter of the entire Australian continent consists of tropical savannas, varying greatly in species composition, geology and climate (Fox et al., 2001). They may have a very high summer rainfall, followed by extreme drought conditions. The woody nitrogen-fixing components of many of them are *Acacia* spp. (sub-genus *Phyllodineae*), often with herbaceous legumes in the wet season. However, in some areas the role of legumes has been usurped by cycads. In Western Australia,

this is usually *Macrozamia reidlei*, which regenerates from swollen roots below soil after fire (Grove et al., 1980), and in the Northern Territory from an arboreal species of *Cycas*, *C. armstrongii*, that produces new growth on aerial stems after fire in a way reminiscent of re-sprouting by eucalypts, which are the major tree component, except that the cycad re-sprouts first (L. Hutley, personal communication).

2.3 Seasonally dry tropical forests (succulent biome)

2.3.1 Caatinga

This type of vegetation is typical of the semi-arid northeast of Brazil, where it covers 850 thousand km^2(Plate 2.8). It is the largest of a number of similar areas in the neotropics (Queiros, 2006). As in the Cerrados, legumes are the most common plants in this vegetation and have been well enumerated (Queiros, 2006). Table 2.2A summarises the genera and species in each sub-family. The genus *Blanchetiodendron* (Mimosoideae) has one species and no report of nodulation, but because of its affinities it is tentatively included with the nodulating group. It is a measure of the amount of work done in this region and in the Cerrados, that this is the only genus whose nodulation status is unknown. Within Caesalpinioideae, the largest number of species (27) are in *Chamaecrista*, with non-nodulating *Senna* (19) and *Bauhinia* (16) also >10. In Mimosoideae, the largest number of species are in *Mimosa* (37), followed by *Calliandra* (12) and *Acacia* (11). In Papilionoideae, there are no genera with more than 9 species present, but in terms

Table 2.2 **A.** Summary of legumes found in the Caatinga region of Northeast Brazil. Data from Queiros (2006). **B.** SDTF of Peru, from Linares-Palomina, 2006 and the RBGE database. Note in the latter that there is one genus of unknown nodulation status and that one of the species of *Acacia* cannot nodulate (see Chapter 1)

Genera		Species	
Nod	Non-nod	Nod	Non-nod
A			
Caesalpinioideae			
2	17	27	64
Mimosoideae			
18	1	90	2
Papilionoideae			
35	4	103	7
B			
Caesalpinioideae			
1	6	1	20
Mimosoideae			
16	1	44	1
Papilionoideae			
16	2+1?	32	2+1?

of total genera and species it is the most common sub-family. Although some of these Caatinga legumes are found in neighbouring vegetation and a few are pan-tropical, more than 50% are endemic to the region. There is also a high level of endemism in the Cerrados, although not all data are available. There are few data on the effectiveness of nodules in the Caatinga, except for some *Mimosa* and *Chamaecrista* species that were studied by Sprent et al. (1996) and E.K. James et al. (unpublished data) as described for the Cerrados in Section 2.2.2. However, the annual rainfall in Caatinga is less that in the Cerrados (300–1000 mm). Endemic species are found in a variety of soils, from rich calcareous areas to sand dunes. There is no obvious pattern of legume distribution among these types. However, there are better possibilities for estimating nitrogen fixation in this area by the $\delta^{15}N$ method, as the soil nitrogen has a higher content of this isotope (R.M. Boddey, personal communication; Unkovich et al., 2008). This suggests that nitrogen cycling in at least some areas of the Caatinga may differ from that in some areas of the Cerrados. How or whether this is relevant to nitrogen fixation is not yet clear.

2.3.2 Other areas

The situation in the SDTF of Peru (another biodiversity hot spot) is broadly similar across sub-families (Table 2.2B), although the total number of taxa is smaller (Linares-Palomino, 2006). There are, however, differences in the genera, with, for example *Chamaecrista* having only one species in Peru, but *Inga* (Mimosoideae), a genus absent from Caatinga, having seven.

2.4 Rain forests

Rain forests are usually associated with the Amazon, tropical Africa and Asia, but are also found elsewhere. Before dealing with the tropical ones, the South American Atlantic forest and temperate rain forests will be considered.

2.4.1 Atlantic forest

This is a 1,233,875-km^2 biodiversity hot spot extending down the Atlantic coast of Brazil from Rio Grande do Norte, to Rio Grande do Sul. It has two parallel parts, the coastal, lowland region and the inland montane and 'Campo Rupestre' region, which extends to Paraguay. It merges with the SDTF region of Brazil, discussed earlier, with which it has many genera and species in common. Again, legumes form the dominant family, with *Inga* being among the most numerous in terms of species. This large genus extends throughout the neotropics and has shown rapid recent speciation (Richardson et al., 2001), a topic that will be covered in Chapter 3. Like the Cerrado and Caatinga regions, it has been decimated by agriculture, this time mainly for sugar cane and coffee growing. The complex nature of the Atlantic forest and its overlap with other regions such as the Caatinga are discussed by Oliveira-Filho et al. (2006). This paper also has appendices with extensive lists of tree species.

2.4.2 Temperate rain forests

Temperate rain forests mainly occur in coastal parts of relevant continents, for example in Western Canada and the Pacific Northwest of the United States, where the prevailing westerly weather brings a high rainfall. However, legumes are rare in these forests, for a variety of reasons, but most probably due to low light levels under conifers. On the other hand, parts of the world heritage temperate rain forest of Tasmania (Australia) have a prominent nodulated legume flora, both trees such as *Acacia melanoxylon* and shrubby, scrambling endemics such as species of *Hovea*. These are found underneath species of *Eucalyptus*, whose isobilateral leaves allow considerable light penetration, even though they are evergreen (personal observations). There are no studies on nitrogen fixation within these areas.

2.4.3 Tropical rain forests

Tropical rain forests are a topic of years of research and numerous publications and it is impossible to summarise the role of the legume component here. Instead, examples will be used to illustrate some of the variations in occurrence of nodulated legumes and possible factors affecting how much nitrogen is fixed. Table 2.3 summarises data from

Table 2.3 Summary of legume genera in three areas of equatorial rain forest. (? indicates nodulation status unknown.) Nodulation is taken to be a generic character

Genera			Species		
Nod	Non-nod	?	Nod	Non-nod	?
A. Borneo (data from the University of Leiden database)					
Caesalpinioideae					
2	18	2	2	83	3
Mimosoideae					
5	2	0	27	8	0
Papilionoideae					
28	1	4	79	1	22
B. Guineo-Congolean (African) forests (data from Lock, 1989)					
Caesalpinioideae					
2	28	3	3	116	88
Mimosoideae					
5	6	4	21	29	9
Papilionoideae					
18	6	7	143	11	14
C. Guyanas and Reserva Ducke (South America) (data from Clarke et al., 2001)					
Caesalpinioideae					
5	27	0	29	86	0
Mimosoideae					
17	1	0	104	9	0
Papilionoideae					
20	5	0	126	11	0

three different areas where the information is sufficiently robust. There is no complete recent flora of China, although there is great international effort underway to produce one. There is an excellent checklist of legumes of South Asia (Kumar & Sane, 2003) and of West Asia (Lock & Simpson 1991), but it has not been possible to sort these into vegetation types. The easternmost of the three examples in Table 2.3 is Borneo followed, in a westerly direction, by the Guineo Congolean region and then a composite South American example. Table 2.3A is derived from the database at the University of Leiden after deleting all those species that appear to have been introduced. Table 2.3B and C are for woody species, including lianes. Data for the Guineo-Congolean forests, which are found throughout equatorial Central and West Africa, are taken from Lock (1989), incorporating taxonomic changes given in Lewis et al. (2005). Major South American tropical rain forests of the Guyanas (including Iwokrama) and the Reserva Ducke in the Terra Firme region of Amazon Brazil are summarised in Table 2.3C. These data are largely taken from Clarke et al. (2001), but the flora of the Reserve Ducke is also comprehensively covered in the monograph edited by Ribeiro et al. (1999).

It must be emphasised that there are major differences within the African and South America forest areas. On the whole, there is less diversity in African than Amazonian rain forests, and this has been linked to climate variables (Parmentier et al., 2007). A separate, but notable difference is that whereas there have been many years of taxonomic study in both regions, in South America, there has also been an emphasis on looking for nodulation – see for example Faria et al. (1989), Moreira et al. (1992), Roggy & Prévost (1999) and Perreijn (2002). In Africa, Corby's work (e.g. 1988) alone is pre-eminent. Thus in Africa and in Borneo there are many genera whose nodulation status is unknown, whereas in South America there are few such genera and none in the regions covered in Table 2.3C. However, even in Africa, many of the genera for which there are no reports, particularly in Caesalpinioideae (Sprent, 2007) are, from their taxonomic affinities, unlikely to be able to nodulate. More than half of the legume genera in the African forest are caesalpinioid, whereas less than half are in the South America forest. Also, fewer of the caesalpinioid legumes in the African forests are able to nodulate. Is this reflected in the contribution of nitrogen fixation to these ecosystems? A very surprising finding of a trip to Cameroon in 2000 was the extent of nodulation on the roots of mature trees and lianas, such as species of *Pterocarpus* and *Mucuna* (Sprent, 2001), often tens of metres from the parent plant. This observation was counter to the usually perceived wisdom that mature trees have a very efficient system for recycling nitrogen and only a few nodules are needed to top up any losses. For the same reason, it is usually recommended that to look for nodulation ability in woody plants, young seedlings should be examined. Sprent (2001) suggested that the profusely nodulated plants may fix enough nitrogen for the ecosystem and that this is transported between plants by mycorrhizas. This suggestion has not been tested in a rain forest, but there is now increasing evidence for nitrogen transfer in both directions between fixing and non-fixing plants (He et al., 2003). This has management implications, if the nodulated trees are selectively logged. It is fair to say that we have no idea how much nitrogen is fixed by legumes in African rain forests. On the other hand, there is evidence from South American forests of all the regions covered in Table 2.3C, as well as in the wider Amazonian region, that significant nitrogen fixation can occur (Martinelli et al., 1992; Moreira et al., 1992; Roggy & Prévost, 1999), although there are many local variations.

In general, potentially nodulated legumes are more likely to do so in seasonally flooded soils than in non-flooded soils (Moreira et al., 1992). The levels of major rivers such as the Amazon and the Orinoco fluctuate by 10 or more metres. In the Orinoco, apparently active nodules can be found on trees at all times (Sprent, 2001). In the Amazon, where the floodwater is rich in nutrients, different species may be active at different seasons. In a detailed study of one area, Kreibich et al. (2006) concluded that the aquatic legume *Neptunia oleracea* fixed significant amounts of nitrogen in what they termed the 'aquatic' phase, whereas various other legumes, mainly trees, were more important during the 'terrestrial' phase. However, their data do not exclude the possibility that nodules on the tree species were active also in the aquatic phase. Unravelling the contribution of legumes to the nitrogen cycle in such areas is made more complicated by high rates of denitrification in the wet season.

2.5 Temperate regions

Legumes in northern temperate areas are almost exclusively papilionoid, although a few nodulated (some herbaceous species of *Chamaecrista*) and non-nodulated (species of *Gleditsia*) caesalpinioids have strayed into North America. In Australia, there are many species of *Acacia*, sub-genus *Phyllodineae*, that occur in the cooler, temperate areas, including rain forest (see above). These, and all the papilionoids of temperate regions, can and usually do nodulate. This section will cover Mediterranean areas, temperate and boreal areas, and high-altitude legumes.

2.5.1 Mediterranean ecosystems

Mediterranean ecosystems are found between 30° and 40° north and south and are characterised by mild wet winters and warm dry summers. Agricultural legumes have been grown in some for millennia, for example the Fertile Crescent in the Middle East, where the cool season grain legumes (peas, faba beans, lentils and chickpeas) are still central to human and animal nutrition. However, there are four other regions of the world where similar conditions prevail, and these are listed in Table 2.4. Area data are from Myers et al. (2000), where all are listed as biodiversity hot spots. IUCN give slightly lower figures for some areas, but either way most of them are very small compared with the ecosystems discussed above. All are on the Western edge of continents where the weather is moderated by cold ocean currents. The native

Table 2.4 Mediterranean ecosystems. Original extent

Geographical region	Approximate area/10^6 km^2
Mediterranean Basin	2.36
Southern California and Baja	0.32
Southwestern Australia	0.31
Central Chile	0.30
Cape of South Africa	0.74

vegetation is evergreen or deciduous shrubland with a high degree of endemism. Nodulated legumes are prominent. Legumes in the Mediterranean Basin, particularly the drier areas, are well researched and will not be considered in detail here. Readers should consult the publications of ICARDA (the International Centre for Agricultural Research in the Dry Areas) with headquarters in Aleppo, Syria, and the outputs from Fabamed, based in France (www.montpelier.inra.fr), which holds regular meetings with publications. All of the regions listed in Table 2.4 have had their original extent reduced greatly, mainly due to agriculture; all have protected areas and it is possible to get an idea of the significance of legumes from these.

Southwest of Western Australia

The Southwest Australian Floristic Region (SWAFR), together with the Cape Floristic Region of South Africa, are different from other Mediterranean ecosystems in that they are on old, highly weathered, nutrient-poor soils, which have been subject to oceanic influence since the Jurassic period. The plant biodiversity of these two regions has been well described by Hopper and Gioa (2004) and Goldblatt and Manning (2002). Lambers et al. (2007) have put forward a scheme to show how plant nutrient-acquisition strategies change with soil age. Although mainly concerned with phosphorus, they also show that nitrogen content of soils is low in very young soils, for example after volcanic eruptions, and in very old, highly weathered soils, peaking in soils of intermediate age. Thus it might be expected that SWAFR has plants with a diversity of nitrogen as well as phosphorus acquisition strategies. Most people know about the unique family Proteaceae that occurs in both SWAFR and the Cape flora. Recently the legume flora has been extensively studied from a taxonomic point of view, but unfortunately there are few studies on nodulation and nitrogen fixation. Within the SWAFR, the Leguminosae is second only in terms of number of species to the Proteaceae, but perhaps even more significant is that only mimosoids and papilionoids are present and all appear to have the ability to nodulate (Plate 2.9). That they do so on soils with very low phosphorus levels goes against the generally perceived wisdom that nitrogen fixation has an inherently high demand for phosphorus. Indeed some legumes (and other plants) from this region cannot tolerate levels of phosphorus that are found in less nutrient-poor soils and Lambers et al. (2007) suggest that these plants may have lost the ability to down-regulate their phosphate uptake systems so that toxic quantities can be taken up. In a detailed global analysis, Houlton et al. (2008) found that the rhizospheres of nodulated plants (legumes and actinorhizas) have high levels of phophatases and suggest that this enables them to access soil phosphorus.

Plants, including legumes in the SWAFR, have many sclerophyll characteristics and are generally drought resistant. Indeed the endemic Australian tribes Mirbelieae and Bossiaeae have recently (3–4 Ma) radiated into arid areas (Crisp et al., 2004; see also Chapter 3). The ability to nodulate and fix nitrogen may be one of a number of characteristics that enable legumes to survive in these rather hostile environments. Many of them produce highly toxic compounds, such as fluoroacetate, to deter herbivores, as well as having phenol-rich, poorly digestible foliage. It has been argued that their rapid accumulation of nutrient-poor biomass, coupled with the low rates of herbivory, provides fuel for the intense fires that rage through the area at intervals (Orians &

Milewski, 2007). Germination of many legume seeds is stimulated by compounds in smoke.

Because it is an ancient ecosystem, parts of which have only recently been converted to agriculture (unlike the Mediterranean Basin), it has been suggested that the SWAFR is an ideal place to study the impacts of agriculture. Webster et al. (2007) investigated possible exchange of pathogens between native and introduced legumes and found, for example, that the native species *Hardenbergia comptonia* house a potyvirus that can damage *Lupinus angustifolius*, a recently introduced crop plant. Conversely, strains of bean yellow mosaic virus, found in various introduced species, can damage the local legume *Kennedia prostrata*. Knowledge of such exchange of pathogens is critical for the management of both native and introduced plants.

Although the nutrient contents of SWAFR and Mediterranean Basin soils are different, they have other features in common, in particular soil acidity. This, coupled with the similar climates has meant that the Australians have mined the Mediterranean Basin and other areas are for legumes and rhizobia that have potential use in Australian agriculture, which still relies heavily on fixed nitrogen. This is an ongoing process – for example the search for new pasture legumes (Loi et al., 2005). Recently, workers in Western Australia have also looked at South African legumes, for example the pasture species *Lotononis angolensis* (Yates et al., 2007), uncovering in the process some new nodulating bacteria (see Chapters 1 and 4).

The Cape Floristic Region

The Cape Floristic Region (CFR) has even more endemic legumes than the SWAFR (Goldblatt & Manning, 2002, chapter 1), but with little work done until recently on their nodulation and nitrogen fixation. Of the four predominantly African tribes of Papilionoideae (Crotalarieae, Hypocalytpeae, Indigofereae and Podalyrieae), Hypocalytpeae is exclusively endemic to CFR as are all but *Calpurnia* in the Podalyrieae. There are also many species of other legume tribes with high levels of endemism. This may be linked to the many different niches arising from the varied topography and soil types (Manning, 2007). Like SWAFR, CFR is also subject to fire, which is an important factor determining floristic composition and its changes with time between fire events (Manning, 2007). All legumes in the CFR (with the exception of *Schotia afra*) and SWAFR appear to be potentially nodulated. One genus, *Cyclopia*, has several species whose leaves are used for the production of honeybush tea (Plate 2.10). At present production is largely on a local scale, harvesting from natural populations, but is beginning to be developed on a farm scale. *Aspalathus linearis* is endemic to this area, but is now grown on a large scale for an international market in rooibos (red bush) tea (Plate 2.11). *A. linearis* grows on soils with very low concentrations of nutrients, whose uptake is aided by the profuse production of cluster roots. Both of these teas are tannin free, a feature used strongly in their marketing (see Section 6.4 in Chapter 6).

2.5.2 Temperate, boreal and high altitude legumes

The majority of legumes occur in temperate latitudes. Although Houlton et al. (2008) concluded that temperature limits nitrogen fixation in higher latitudes, all legumes

native to these regions are potentially nodulated (Chapter 1). Many have been used in agriculture for centuries and thus have been well studied. Indeed, nitrogen fixation research had its origins in these areas well over a century ago (Nutman, 1987). In spite of this, beyond the recording of nodulation and development of inoculants for a few species, very little is known about how much nitrogen is fixed or with which bacteria.

In the Southern Hemisphere, New Zealand has very few native legumes, but quite a few nodulated actinorhizal plants; islands such as the Falklands (Malvinas) have neither. Temperate Australia has a wealth of legumes, mainly acacias and endemic papilionoid species. Both nodulation and rhizobia have been well studied in acacias, generally with a view to their being used for land reclamation and farm forestry, reviewed by Brockwell et al. (2005). As indicated above, there are relatively few studies on native papilionoid legumes, although there is now an increasing interest. To date, all endophytes have been classified as α-rhizobia, both fast and slow-growing (Lafay & Burdon, 1998).

In the Northern Hemisphere, there is interest in North American genera that can fix nitrogen in boreal areas. Both hosts and their rhizobia are well adapted to their environment For example, Poinsot et al. (2001) found that a strain of *Mesorhizobium* nodulating *Oxytropis arctobia* in Northern Canada had a modification to its Nod factor (see Chapter 5) giving cold tolerance. *Oxytropis* is one of a number of papilionoid genera with species near or within the Arctic circle (Sprent, 2001), They are all perennial herbs, frequently rhizomatous and rapidly generate new growth in spring. In Europe, grain legumes are widely grown, usually nodulating effectively with local rhizobia, but there has been little work on their nodulation since the book edited by Jones & Davies (1983). There is some renewed interest in pasture species for sustainable agriculture, especially in Scandinavia where forage legumes are important for cattle, but again the number of species covered is very limited, mainly *Trifolium repens*, *T. pratense* and *Medicago sativa*, and, to a lesser extent *T. hybridum* and *Lotus corniculatus* (Frankow-Lindberg et al., 2005). However, the total number of native legumes in Great Britain and Northern Europe is relatively low, consisting of about 24 genera (133 spp.) from 6 papilionoid tribes (Table 2.5)

In Asia there is now interest in some harsh areas, notably in mainland China, where studies of native legumes on the Qinghai-Tibet Plateau and elsewhere are being carried out (Plate 2.12). Many of these areas have a long history of agriculture and have become degraded as a result of grazing pressure. *Vicia faba* has been grown in China for over 4000 years and now accounts for nearly half the world's production of this crop (Tian et al., 2007). Different rhizobia nodulate the crop in different ecological regions. In the Qinghai-Tibet plateau, where faba beans have been grown for only 2000 years, it is nodulated by *Rhizobium leguminosarum*, which was also found to nodulate species of *Oxytropis* and *Medicago archiducis-nicolai* (Kan et al., 2007). These workers also looked at nodulation in 21 legume species from the area and the nearby Loess Plateau and found a range of rhizobia in them, These plateaux are 4000 to 6000 metres above sea level, having low oxygen levels, high irradiation, low temperature and often also salinity. Some of the strains isolated were tolerant of high pH and salinity. In other parts of central Asia, there are numerous genera with species growing at altitude, but apart from registering their occurrence, little is known about them. Table 2.6 lists some of the genera recorded in *Legumes of Northern Eurasia* (Yakovlev et al., 1996).

Table 2.5 Legumes native to Great Britain and Northern Europe. Data on genera and species modified from Blamey and Grey-Wilson (1989) to take into account taxonomic changes in Lewis et al. (2005)

Tribe	Genus	Species
Fabeae	*Lathyrus*	16
	Vicia	20
Galegeae	*Galega*	1
	Colutea	1
Genisteae	*Cytisus*	3
	Genista	3
	Lembotropis	1
	Spartium	2
	Ulex	3
Hedysareae	*Onobrychis*	1
Loteae	*Anthyllis*	1
	Coronilla	4
	Dorycnium	1
	Hippocrepis	1
	Lotus	5
	Ornithopus	3
	Tetragonolobus	1
Trifolieae	*Medicago*	7
	Melilotus	5
	Ononis	6
	Trifolium	30
	Trigonella	3

Table 2.6 Some genera of legumes from Northern Eurasia that have species growing at altitude and in deserts. Data from Yakovlev et al. (1996), with number of species from Lewis et al. (2005). All are papilioinoid

Genus	Species	Comment
Ammodendron	4–5	Drought and saline tolerant
Ammothamnus	~2	Drought and saline tolerant
Astragalus	2500+	Centre of diversity in arid continental middle Asia and the plateau of Iran
Chesneya	~30	Centre of diversity in Central Asia, some alpine spp. grow up to 5000 m (Jacquez & Patten, 1996)
Eremosparton	3	Desert shrubs
Gueldenstaedtia	~30	Some species grow up to 3000 m
Oxytropis	300–400	Main centre of diversity in cold interior Asian plateaux, some circumpolar; some xerophytic
Tibetia	4	Not in Yakovlev et al. (1996). Segregated from *Gueldenstaedtia* (Lock & Schrire, 2005). Mainly alpine
Trifolium	~250	Some alpine species

Legumes occur at high altitude in other areas, of which the Andes have received the most attention. Here lupins are common (Plate 2.13). These mountains are the most species-rich of any tropical mountains, and the species there must have colonised the area over the last 2 to 4 Ma. Hughes and Eastwood (2006) found a monophyletic group of 81 species of *Lupinus*, which they estimated to have arisen over the last 1.18 to 1.76 Ma, thus given them the record for the fastest rate of evolution yet found in plants. Geographic isolation was a major contributory factor to this rapid speciation. Physiologically, how nodules, whose operation depends on correct gas pressure (Chapter 5), operate at such low pressures is completely unknown. Indeed there is little knowledge of how any plant processes are affected by altitude. High-altitude legumes are usually nodulated papilionoids, a few Andean species of *Senna*, a non-nodulating genus, being the exception (C.E. Hughes, personal communication).

2.6 Invasive legumes

Invasive plants and animals are receiving a great deal of attention, as the extent of their occurrence and effects on the environment become clearer. Among plants, there are numerous cases of invasive legumes. Some such as *Ulex europeaus* (gorse) and *Cytisus scoparius* (broom) were introduced into Australia and New Zealand by early settlers and have since been classified as noxious weeds. Broom has also invaded large areas of the Pacific Northwest of the United States, where it acidifies the soil and affects nutrient cycling (Caldwell, 2006). Gorse is also a major problem in volcanic soils of Hawaii (Leary et al., 2006b). Both these shrubby legumes produce large quantities of seed, making eradication difficult. They also appear to nodulate freely wherever they occur. In wetter areas of Hawaii, the large, fast-growing nodulated tree, *Falcataria moluccana*, has transformed the *Metrosideros* forest so much that it is suggested that it be considered a completely different ecosystem (Hughes & Uowolo, 2006). A native annual legume in Hawaii, *Chamaecrista nictitans*, by enriching the soil in nitrogen after its death, is thought to facilitate invasion by alien grasses (Carino & Daehler, 2002). Arguably one of the fastest-growing legumes known, *Pueraria montana* (Kudzu), was introduced into the United States in 1876, used to control erosion, but has been so successful that in 1997 it was classed as a noxious weed. Although it is known to be efficient at fixing nitrogen, and appears to nodulate freely, very little else is known as to its effects on native ecosystems (Forseth & Innis, 2004). Similarly invasive *Mimosa* species may be successful because of their ability to nodulate with local strains of *Burkholderia* (Chen et al., 2005). *Lupinus nootkanensis*, the Alaska lupin, has been introduced into Iceland where it is variously regarded as a benefit (because of ability to nodulate and to extract phosphorus form low-phosphorus soils) or as a threat to natural ecosystems, because it is very invasive (Plate 2.14). Parker et al. (2006) showed that, in some cases, the invasiveness of legumes (including *Cytisus scoparius*) could be limited by the availability of suitable rhizobial symbionts. In a detailed meta-analysis of invasive plants, Liao et al. (2007) showed that ability to fix nitrogen had a major effect on ecosystem carbon and nitrogen cycles. Australia has been exporting acacias around the world for years and in some places, such as South Africa, they are becoming

a serious threat, particularly because of their high water use (e.g. Le Maitre et al., 2002). It is now being realised in Australia, that before introducing species to new areas, potential problems should be addressed (Paynter et al., 2003). At a time when *Leucaena leucocephala* was being widely trumpeted as the answer to all agroforestry problems in developing countries, Hughes & Styles (1989) advocated a careful cost benefit analysis.

Chapter 3

Evolution of Nodulation

The first part of this chapter will concentrate on the plant side of the symbiosis, considering in turn, when, where, how and why many legumes adopted a symbiotic life style with soil bacteria. This is followed by a short section on the bacterial partner and ends with a brief consideration of the role of 'model legumes' in unravelling some of the major questions of nodule formation.

3.1 When did nodulation first occur?

Nodulation is a phenomenon restricted to the Eurosid 1 clade of angiosperms (Fig. 3.1). Although not included in this analysis, *Parasponia*, the one non-legume known to nodulate with rhizobia, is in the Rosales. When the ancestors of this clade first appeared is not entirely clear, but was likely to have been at least 100 million years ago. For a discussion of this and when plants nodulating with *Frankia* (actinorhizal plants, shown in bold in Fig. 3.1) may have evolved, see Swensen and Benson (2007). Why the occurrence of actinorhizal symbioses is so scattered is unclear, as is why only one of the two main branches of the Fabales led to nodulation. Even within this nodulating branch (the Leguminosae) things are far from simple.

A great deal of research has been conducted over the last 15 or so years, matching molecular, morphological and anatomical data to produce possible legume phylogenies. Based on these data and taking into account well-established legume fossil data to root trees in a likely time frame, Lavin et al. (2005) published a scenario for the evolution of the major tribes of legumes. Evidence suggests that the first legumes appeared about 59 Ma, in the early Tertiary period, rather than in the late Cretaceous period as once thought. Within the next 1 to 2 million years, elements of caesalpinioid and papilionoid legumes evolved, with mimosoids branching from the caesalpinioids rather later (about 42 Ma). The chronology of the major events involving nodulation is summarised in Table 3.1.

The total number of species analysed by Lavin et al. (2005) is impressively large, but does not include some important nodulating genera. In Caesalpinioideae, only

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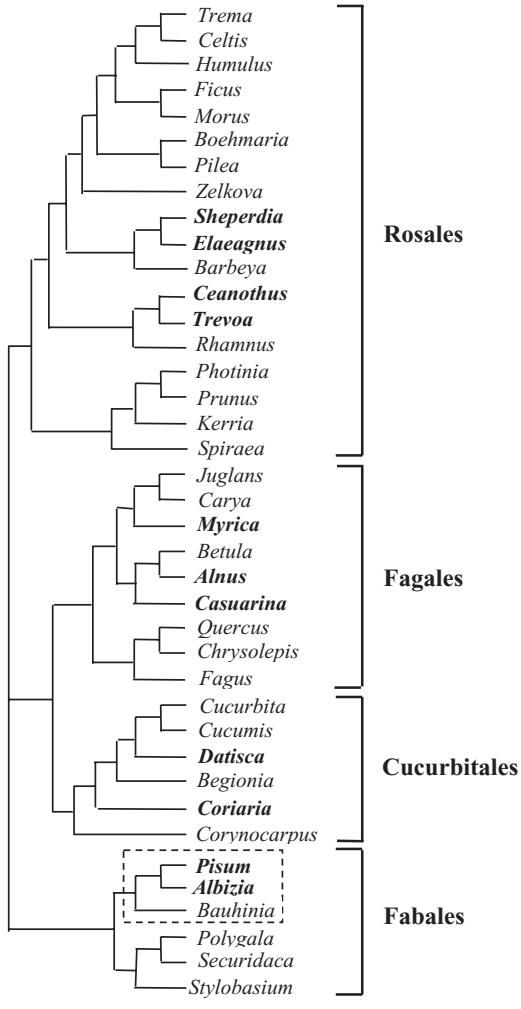

Figure 3.1 The nitrogen-fixing part of the Eurosid I clade, after Soltis et al. (2000). Actinorhizal genera in bold type. Legumes in box with dashed outline.

Chamaecrista fasciculata is represented. This is in a branched group evolving about 54.5 Ma and including genera shown in Fig. 1.3 (p. 6) under Cassiinae and some Caesalpineae. These groups also include non-nodulating genera. It is simpler at present to infer a single nodulating event in this group, but when there is better resolution, it may well emerge that there are two, one each in the Cassiinae and Caesalpinieae, as suggested by Doyle and Luckow (2003), who also linked one of these nodulating events to the mimosoid lineage. Bruneau et al. (2008) carried out a detailed analysis of Caesalpinioideae, with some species of other sub-families being included. Molecular and morphological characteristics were included and, like Lavin et al. (2005), legume fossils were used to put data into a possible time frame. However, they excluded some

Table 3.1 Chronology of crown nodes of selected groups of nodulated legumes. Data from Lavin et al. (2005)

Major group	Mean age (Ma)	Standard deviation of mean
Leguminosae	59.0	0.2
Papilionodeae	58.6	0.2
Genistoids	56.4	0.2
Dalbergioids	55.3	0.5
Nodulated Caesalpinioideae	54.5	0.4
Swartzia	48.9	2.8
Mirbelioid	48.4	1.3
Robinioid	48.3	1.0
Millettioid	45.2	1.7
Mimosoideae	42.4	2.6
IRLC	39.0	3.2
Nodulated mimosoids (most)	33.2	3.2
Indigoferoid	30.0	3.3
Phaseoloid group	27.8	1.6

and included other fossils than those used by Lavin et al. (2005). As a result their time span begins rather earlier, by about 5 million years. The Bruneau et al. (2008) paper sheds considerable light on relationships within Caesalpinioideae, but, as the authors hint, it does little to clarify the position with respect to origin of nodulation within this group, except perhaps to support the idea of two or more nodulation events.

It is generally agreed that Mimosoideae is sister to Caesalpinioideae and evolved at a later stage (Lavin et al., (2005). As discussed in Chapter 1, all the non-nodulating genera (apart from some that may have lost this ability) are currently placed in tribe Mimoseae, although it is recognised that, until more data become available, this tribe is one of convenience (Luckow, 2005). In Lavin et al. (2005), there are two branches from the mimosoid crown node, dated at 42.4 Ma. One includes only the genus *Pentaclethra*, one of the few genera that are known to have both nodulating and non-nodulating species (Chapter 1). The other branch also has two parts, the first (and smallest) consisting of eight genera, two of which (*Piptadeniastrum* and *Entada*) nodulate, one (*Pseudoprosopis*) for which there is no information and with the rest (*Amblygonocarpus, Adenanthera, Tetrapleura, Xylia, Calpocalyx*) appearing unable to nodulate (Sprent, 2001). Other non-nodulating genera from tribe Mimoseae are not represented in the Lavin et al. (2005) analysis. All the nodulating genera sampled, from all mimosoid tribes, are in a major branch with a crown node dated at 33.2 Ma. The Bruneau et al. (2008) chronology is similar to that of Lavin et al. (2005). Thus there appears to be a basal group of mimosoid legumes that generally lack the ability to nodulate, as discussed in Sprent (2001). How the occurrence of nodulation in Mimosoideae relates to that in Caesalpinioideae is unclear. However, it is of interest and may be relevant, that in both sub-families, non-nodulation is much more prevalent in Africa than in the Neotropics. *Parkia* is a genus that once had its own tribe, but is now included in Mimoseae. It is the only genus in the main nodulating section of Mimosoideae that appears not to nodulate, although some species of *Acacia* may have lost this ability (Chapter 1).

In the analysis of Bruneau et al. (2008), the origin of Papilionoideae is placed later (45 Ma) than that of Lavin et al. (2005), but as they point out, very few samples were included. Here the estimates of Lavin et al. (2005) are used. In Papilionoideae, again there are basal groups that lack the ability to nodulate, most notably the non-nodulating branch of the Swartzioid group and the branch labelled 'various' that covers non-nodulating members of tribe Sophoreae and related tribes (Fig. 1.3). Again two nodulating events are possible. Following the second of these events, all subsequent branches are nodulated, except in the few cases where nodulating ability has been lost. The genistoid and dalbergioid nodes are dated at 56.4 and 55.3 Ma, respectively (Lavin et al., 2005) (Table 3.1). In species that have been studied in tribes Crotalarieae and Genisteae, nodules are formed following direct epidermal penetration, newly infected cells divide repeatedly, so that infected tissue contains few or no uninfected cells and transcellular infection threads are not seen (Sprent, 2007 and references therein; see also Fig. 5.1 of the present book). Aeschynomenoid nodules are defined by having an infection via cracks where lateral or adventitious roots emerge and again, newly infected cells divide repeatedly, uninfected cells in the infected region are rare or absent and transcellular infection threads are not seen. The major difference between these two groups is that the former has indeterminate nodule growth and the latter determinate growth (Figs. 1.1 and 1.2). These features led Sprent (2007) to hypothesise that the earliest nodules were formed following direct infection through wounds or epidermis and that infection threads were a later development, necessary before the familiar root hair infection mechanism could occur and bacteria could be transmitted across cells by transcellular infection threads. There are several cases of extant legumes where infection threads are formed following a non-hair infection. In the Mimosoideae, aquatic species of *Neptunia* have a crack infection, very similar to that found in aeschynomenoid nodules, followed by formation of infection threads (Subba-Rao et al., 1995); in *Mimosa scabrella* infection may occur between epidermal cells, with infection threads being formed later (Faria et al., 1988) and subsequent nodule development proceeding as in some other species of *Mimosa* with a root hair infection (Elliott et al, 2007a). *Lonchocarpus muehlbergianus* (tribe Millettieae) was found to lack root hairs and infection was thought to occur through epidermal cells, with later development of transcellular infection threads and formation of infected tissue with both infected and uninfected cells (Cordeiro et al., 1996). There are also several reports of legumes that normally have a root hair infection bypassing this process under certain conditions, for example waterlogging in the case of *Lotus uliginosus* (James & Sprent, 1999). *Sesbania rostrata* may adapt both its infection process and nodule development (determinate or indeterminate) according to whether it is waterlogged or not, but in both cases transcellular infection threads are formed during nodule development (Goormachtig et al., 2004). The versatility of nodulation processes in these legumes from widely different taxonomic groups underlines the suggestion that the primitive state is a non-hair infection, which is used as a fallback process under certain forms of stress, especially waterlogging (Goormachtig et al., 2004). Unfortunately there is no information on the infection of caesalpinioid legumes by rhizobia. The ideas outlined above are summarised in Fig. 3.2. Comparing this diagram with the chronology given in Table 3.1 shows that, in addition to the major groups of legumes that had their origin around 55 Ma, a further group originated in the next 10 million years. This was

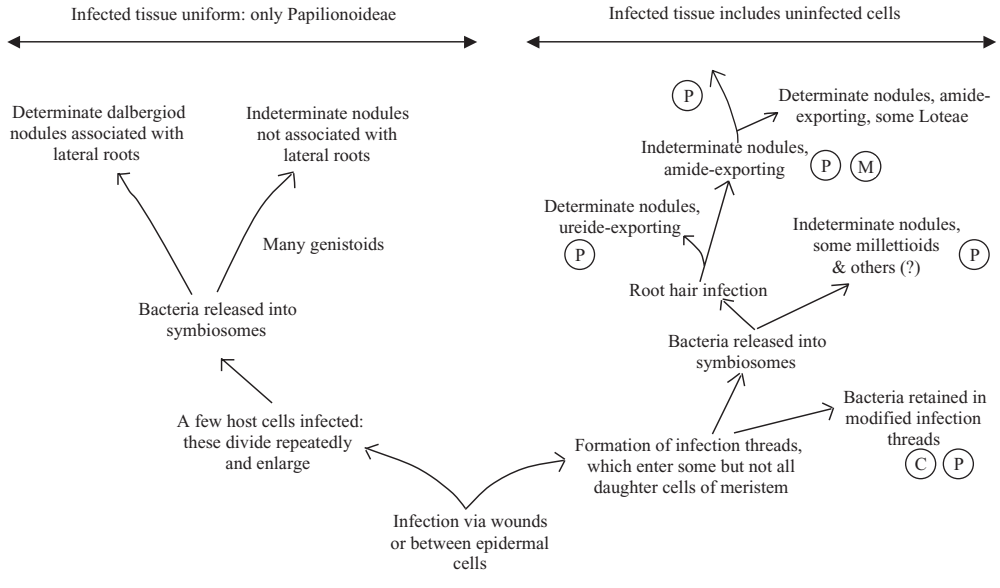
Infected tissue uniform: only Papilionoideae
Infected tissue includes uninfected cells
Determinate dalbergiod nodules associated with lateral roots
Indeterminate nodules not associated with lateral roots
Many genistoids
Bacteria released into symbiosomes
A few host cells infected: these divide repeatedly and enlarge
Infection via wounds or between epidermal cells
Formation of infection threads, which enter some but not all daughter cells of meristem
Bacteria released into symbiosomes
Root hair infection
Determinate nodules, ureide-exporting
P
Indeterminate nodules, amide-exporting
P M
Determinate nodules, amide-exporting, some Loteae
P
Indeterminate nodules, some millettioids & others (?)
P
Bacteria retained in modified infection threads
C P

Figure 3.2 Possible stages in the evolution of extant legume nodules. Encircled upper-case letters indicate the sub-family where the feature is found. Modified from Sprent (2007).

a time of repeated wide fluctuations in temperature and rapid divergence of legumes (Schrire et al., 2005). All nodulated legumes having their origin later than 40 Ma have a root hair-based infection process, even though this may not always be expressed. The large phaseoloid group (tribes Desmodieae, Phaseoleae and Psoraleae, Table 1.15) had its origin about 28 Ma. With a few exceptions its members are herbaceous, lianes or small shrubs. Extant species are spread more or less evenly across tropical continental regions, the majority being in the grass biome (Schrire et al., 2005). Here their unique determinate, ureide-exporting nodules (Chapter 5) appear to have given them a distinct advantage, although it is unclear what this is. It has been suggested that allantoin and allantoic acid (the ureides) have the benefit of being economical with carbon, compared with amides, but the disadvantage of being poorly soluble at lower temperatures (Sprent, 1980).

3.2 Where did nodulation first occur, and where are nodulated legumes going?

The earliest idea was that legumes evolved in the humid tropics when Africa and South America were still joined, enabling taxa to move readily across continents. However, these two continents are now known to have separated before legumes evolved, so an alternative was proposed in which legumes moved between South America and Africa via a northerly land bridge (the boreal hypothesis). These ideas have been well

described by Doyle and Luckow (2003). More recently Schrire et al. (2005) pointed out some anomalies in legume distribution that did not support the boreal hypothesis. Instead they suggested that legumes could hop across islands or otherwise be carried by wind or sea water (see also Renner, 2004a) or by extreme weather events (Sprent, 2007). Schrire et al. (2005) further carried out a very comprehensive analysis of where extant legume genera are found. As a result they suggested that the current distribution may be more related to particular biomes (see Chapter 2), where genera and species have arrived by dispersal, than to vicariance, where species evolve following geographic isolation. In addition they suggested that rather than evolving in the humid tropics, legumes arose in a semi-arid area just north of the Tethys Sea, which separated the two major land masses existing at that time. The earliest legumes were adapted to semi-arid conditions (the succulent biome) and subsequently spread into arid, fire-tolerant areas (the grass biome), into humid areas (rain forest biomes) and into north and south temperate areas (Chapter 2). These movements occurred while land masses were also moving and were related to major climatic shifts. Schrire et al. (2005) list a set of characteristics found in fossil legumes that are consistent with a semi-arid environment and that are found in extant legumes in such areas. These include compound leaves, which can be shed in part or completely during periods of drought. In extant SDTF there is a mixture of nodulated and non-nodulated legumes, as there appears to have been in the original biome north of the Tethys Sea. An interesting question is when legumes diversified into the grass biome, which could have been comparatively recently, since C_4 grasses evolved less than 10 Ma (Sprent, 2007). Whenever it was, few non-nodulating genera appear to have made this move (Chapter 2). This contrasts with rain forests, where there are numerous non-nodulating genera, with major groups still actively evolving. As mentioned in Chapter 2, virtually all legumes in temperate biomes are nodulated.

3.2.1 Madagascar as a special case

In a comprehensive review of vicariance versus dispersal as ways of explaining the present diversity of animals and plants in Madagascar, Yoder and Nowak (2006) point out the many sister groups between Africa and Madagascar. As far as higher plants are concerned the picture is complex. It is generally agreed that Madagascar separated from the main Indian land mass about 88 Ma. Molecular analysis of the widespread Asian ectomycorrhizal family Dipterocarpaceae suggests that extant species of this and the derived family Sarcolaenaceae (endemic to Madagascar) arose from ancestors present before the separation (Ducousso et al., 2004). However, as discussed above, legumes evolved after the separation of these two land masses, making the situation more complex. Fortunately there is a comprehensive work on the legumes of Madagascar (Du Puy et al., 2002), and this will be used here to highlight some of the problems. Table 3.2 summarises the native legume species found there, most of which are endemic. All the genera specified in the comments column apart from *Viguieranthus* (which is endemic to Madagascar) and *Mimosa* are well represented in Africa and have probably arrived from there. Indeed, as has been suggested for members of family Melastomataceae (Renner, 2004b), each genus may have made several separate trips. For example, four such transfers have been suggested for *Indigofera*, possibly in the

Table 3.2 Legumes native to Madagascar, most of which are endemic. Data from Du Puy et al. (2002)

Tribe	Genera	Species	Comments
Caesalpinieae	7	17	Includes one sp. of *Erythrophleum*, nodulated (?)
Cassieae	7	30	Includes 9 spp. of *Chamaecrista*, all nodulated (?)
Cercideae	2	17	
Detarieae	5	16	
Ingeae	2	45	*Albizia* and *Viguieranthus*
Mimoseae	10	80	Includes 31 *Mimosa* spp.
Abreae	1	7	
Aeschynomeneae	8	27	Included in Dalbergioid clade in Chapter 1
Crotalarieae	2	42	Includes 41 *Crotalaria* spp.
Dalbergieae	1	25	
Desmodieae	5	18	
Genisteae	1	3	
Indigofereae	4	64	Includes 44 *Indigofera* spp.
Millettieae	10	71	Includes 27 *Tephrosia* spp.
Phaseoleae	19	61	
Sesbanieae	1	3	
Sophoreae	8	17	A mix of nod- and non-nod genera
Swartzieae	1	2	Non-nodulating
Trifolieae	1	1	

last 10 Ma; on each occasion new species developed within Madagascar (B.D. Schrire, personal communication). This genus, together with *Tephrosia* and *Crotalaria*, both of which are shrubs or herbs, have species that can grow on very nutrient-poor soils. *Crotalaria* species are known to nodulate with a range of α-Proteobacteria (Chapters 1 and 4). In view of the fact that Malagassy species occur on almost all types of soil and habitat (Du Puy et al., 2002), it would be interesting to see if particular endosymbionts are associated with certain soil conditions as has been suggested for the related genus *Lotononis* (Yates et al., 2007). Seven different genera of α- and β-Proteobacteria have been isolated from nodules of *Dalbergia* spp. from Madagascar (Rasolomampianina et al., 2005). *Erythrophleum couminga* (Caesalpinioideae) only occurs in the western coastal region of Madagascar and is thought to be closely related to the East African species, *E. suaveolens*, known to be nodulated. The big puzzle concerns *Mimosa*, which has 31 species in Madagascar, but which is very poorly represented in Africa, with at most 4 native species (M. Simon, personal communication), including *M. busseana* from Tanzania and Mozambique (Lock, 1989), other species being introduced. There are 5 species in Asia, with the remaining nearly 500 species from South America (M. Simon, personal communication). How the genus arrived in Madagascar is very unclear, but it clearly found conditions to its liking as it occurs throughout the island. Twelve new species are described in Du Puy et al. (2002). How many arrivals and from where they came is likely to remain unclear until a detailed molecular analysis is carried out. At least one Madagascan species, plus species from Nepal, introductions from Vietnam, Australia, Taiwan and its native Brazil, are nodulated by β-Proteobacteria (Elliott et al., 2007a) (Chapter 4).

3.2.2 Recent evolution

Evolution of legumes is still occurring, both by dispersal and vicariance and some examples are given in this section. In the species-rich neotropical genus *Inga* (Mimosoideae), speciation appears to have been concentrated in the last 10 million years, with a significant number of species being as recent as 2 Ma. Factors causing this increase in diversity include rapid changes of climate in tropical areas, closing of the Isthmus of Panama, and the uplifting of the Andes (Richardson et al., 2001). It has recently been suggested that this uplifting took place at a particularly rapid rate (1.5 km in a million years) about 8 Ma (Garzione et al., 2008) although the interpretation of isotope data leading to this conclusion has still to be tested (Kerr, 2008). Uplifting of the Andes allowed the most rapid evolution of species yet known for plants, in *Lupinus*. Eighty-one species of lupin have evolved in the high Andes (see Chapter 2) in less than the last 2 million years. This equals the record for eukaryotic diversification, held by cichlid fish in East African lakes (Hughes & Eastwood, 2006). The high plateaux of the Andes were likened to islands in their isolation, allowing rapid evolution. A similar situation obtains in parts of Northern Eurasia, where genera such as *Hedysarum* are undergoing speciation, and in the islands of the Russian archipelago, above 80° north, where *Astragalus*, *Oxytropis* and *Hedysarum* have distinct species (Yakovlev et al., 1996). In Australia, members of the endemic tribes Mirbelieae and Bossiaeae are diversifying into areas of increasing aridity (Crisp et al., 2004). Crisp & Cook (2007), in a comprehensive examination of the Southwestern and Southeastern Australian flora, concluded that a vicariance event associated with the formation of the Nullabor Plain led to speciation of genera in these two legume tribes about 2 to 4 Ma. In a detailed study of the neotropical dalbergioid genus *Platymiscium*, Saslis-Lagoudakis et al. (2008) concluded, inter alia, that this genus originated in seasonally dry tropical forests and then invaded the Amazon region twice within the last 5.6 million years. This is consistent with the suggestion of Schrire et al. (2005) that legumes evolved in arid areas and later colonised the wet tropics.

It should be emphasised that as more data become available ideas may change. For example, it is commonly thought that the species-rich Cape Floristic region of South Africa (see Section 2.5.1) resulted from the development of a Mediterranean climate about 5 Ma. However, recent work on two legumes tribes Crotalarieae (pro parte) and Podalyrieae has cast some doubt on this, suggesting that they may be much older, 44 to 46 Ma (Edwards & Hawkins, 2007).

3.3 How was the information for nodulation acquired?

There are two major routes by which acquisition of the information for nodulation may have occurred. One involves recruitment of genes that evolved for other purposes, and the other involves genes that have been duplicated, with some of the duplications being modified for use in symbiosis (Sprent, 2008).

3.3.1 Ancient genes that have been recruited for symbiotic purposes

With the exception of lichens, the first symbioses to have evolved between green plants and fungi were arbuscular mycorhizas (AM). Fossil evidence for these dates

back at least 400 Ma (Remy et al., 1994), and it is thought that AM were needed by plants to enable them to obtain nutrients from the inhospitable terrestrial environment that they were beginning to colonise. These early plants had no roots and AM were formed on both above and below ground axes (Nicolson, 1975). It has been known for many years that some aspects of the signalling process leading to AM have common features with early stages of nodulation (Szczyglowski & Amyot, 2003) as well as other colonizing rhizobacteria (Sanchez et al., 2004). The plant gene *SYMRK* is involved in this process. Versions of this gene, which is found in all AM plants tested, generate products that vary in length, with some parts being intra- and others extracellular. Markmann et al. (2008) analysed the products of this gene in plants of the Eurosid 1 clade (Fig. 3.1), including actinorhizal and legume nodulating species and also non-nodulating species from the same clade. All had a longer *SYMRK* product than plants from outside the clade. By making a series of transgenic constructs between different species of plant they showed that this longer product was necessary for nodulation in both actinorhizal and legume plants. A shorter product was sufficient for AM formation. This important observation paves the way for further understanding the particular properties of the Eurosid 1 (nodulating) clade. *SYMRK* acts on an early stage of nodulation and is independent of type of nodule formed or specific host-rhizobial combinations. A pair of genes known as *CASTOR* and *POLLUX* are also implicated in both AM and nodule formation, being involved in the entry of symbionts into plant cells. These genes are unusual in being located in root plastids (Imaizumi-Anraku et al., 2005). In view of the relations between nodules and roots, is there anything special about root development in the Eurosid I clade? In an extensive analysis of the organisation of apical meristems of roots in 132 families of angiosperms, none was apparent (Heimsch & Seago, 2008; J.M. Seago, personal communication).

One difference between legume and actinorhizal nodules that has fascinated people for many years is the fact that the former have some shoot-like features, most notably a peripheral vascular system, whereas the latter are more root-like with a central vascular system. Pawlowski and Sprent (2007) have made a detailed comparison between these two types of nodule. It has been known for many years that roots can grow out of legume nodules, usually older ones (Sprent, 2001). More recently, Ferguson & Reid (2005) studied a mutant of pea that could form hybrid nodule/root structures, in which both the root and nodule parts were functional. The *LATD* gene of *Medicago truncatula* is necessary for proper development of both lateral roots and nodules (Bright et al., 2005). Considering the known role of plant hormones in the development of both of these structures, sometimes acting in opposite directions (e.g. cytokinins, Lohar et al., 2004) alterations in hormone balance are a likely cause of switching the balance between formation of nodule and root structures. Kondorosi et al. (2005) point out that lateral roots and nodules are formed on different regions of the growing tap root and thus may be expected to have different hormone levels.

3.3.2 Gene duplication

Pink colouration in the centre of legumes nodules has been used for many years as a likely indication of active nitrogen fixation (Chapter 5). (Leg)haemoglobin that causes

this colouration has also been widely studied, as has its role in facilitating oxygen diffusion and, more recently for interacting with nitric oxide metabolism (reviewed in Minchin et al., 2008). Haemoglobins are of ancient origin (over 1500 Ma), and during evolution genes coding for them have separated into many branches within a superfamily (Wittenberg et al., 2002). They appear to occur in all angiosperms in two gene/protein families, containing symbiotic and non-symbiotic forms, respectively. The latter may have a role in AM as well as nodules (Vieweg et al., 2004). Most legumes have several forms of symbiotic haemoglobin and recent work has found that these are produced sequentially, coupled with the induction of genes associated with nitrogen fixation (Downie, 2005; Ott et al., 2005). A possible intermediate form, found in a species of *Chamaecrista*, is discussed in Section 3.5.

Comparisons have been made between the growth of a pollen tube down a style and the formation of an infection thread in root hairs. Both are a form of tip growth, involving enzymes that degrade cell walls, such as polygalacturonase and cellulose, and it has been suggested that the processes may involve genes that have been duplicated in the past (Rodriguez-Llorente et al., 2004). Manoury et al. (2008) point out the difficulties of taking this analogy too far. These include the fact that infection thread growth occurs against the turgor pressure of the root hair (see Section 5.1), whereas there is no pressure barrier for pollen tube growth.

Relatively early in the evolution of papilionoid legumes (about 50 Ma) the whole genome was duplicated (Pfeil et al., 2005). Did this genome duplication event introduce the flexibility that enabled the evolution of the different types of nodule growth (determinate, indeterminate) and different types of nodule metabolism (amide versus ureide export) to evolve? There have subsequently been other gene duplication events, for example in soybean at about 3 to 5 Ma (Schauser et al., 2008), but their significance for nodulation processes (if any) is unclear. It is known that the information for the formation of both determinate and indeterminate nodules in the absence of rhizobia is found in the genomes of four species of papilionoid legume, including the two model legumes, *Medicago truncatula* and *Lotus japonicus* (Gleason et al., 2006; Tiricine et al., 2006; see also Sprent & James, 2007).

One developmental process that has been demonstrated for lupinoid (*Lupinus albus*) desmodioid (*Lotus japonicus*) and indeterminate (*Medicago truncatula, M. sativa*) nodules is a high degree of endoreduplication in the infected cells (reviewed in Manoury et al., 2008). Endoreduplication is also a feature of the giant cells of galls formed on plants by nematodes and may be, at least in part, under the same host genetic control (Mathesius, 2003). This paper also gives a comprehensive comparison of the role of hormones and other factors in lateral root, root nodule and nematode gall formation. Giant cells of nematode galls, unlike the infected cells in legume nodules, are also transfer cells (i.e. their walls have many projections facilitating solute exchange with neighbouring cells). Transfer cells in legume nodules are relatively uncommon, only occurring in some tribes and associated with vascular bundles (see Section 5.6). Like bacteria, nematodes tend to have a bad press, because of the diseases they cause. It has been suggested that plant parasitic nematodes may have developed from saprophytic forms, after acquiring the genetic information for producing phytohormones (Bird & Kaloshian, 2003). Further, some of the genes associated with gall formation appear to have been acquired from soil bacteria including rhizobia (Bird et al., 2003).

It has been suggested that root nodule bacteria evolved from parasitic forms, largely because *Rhizobium* and the gall-forming *Agrobacterium* are so closely related (possibly con-generic; see Chapter 4) (Sprent & Raven, 1985). This is also consistent with the primitive mode of infection not being through root hairs, as agrobacteria are wound pathogens. However, there are also problems with this suggestion, including the fact that agrobacteria transfer phytohormone-coding DNA into host cells (Sprent & Raven, 1992). Also on the bacterial side (see Chapter 4), it has generally been assumed that, in order to infect plants, rhizobia must have the so-called common nodulation genes, *nodABC*. However, it has recently been shown that some photosynthetic bacteria nodulating stems of two species of *Aeschynomene* lack these genes, but are not defective in nodulation (Giraud et al., 2007). This again is consistent with the non–root-hair infection pathway being ancestral to the hair infection pathway.

Early in plant evolution, at least when meristems were formed, signalling molecules (hormones) were needed. All currently known plant hormones appear to have a role in nodule formation: these are summarised in Table 5.2 (p. 82) and are discussed in more detail in Manoury et al. (2008) and in Chapter 5. Plant hormones are also produced by many soil bacteria, including rhizobia, and these too may affect nodulation processes. A recent noteworthy result suggests that bacterial cytokinins may be a key to nodulation in Nod factor-independent nodulation, such as that described for *Aeschynomene* above (Frugier et al., 2008).

Flavonoids are secreted by roots of many vascular plants, and in the case of legumes have been recruited to act as signal molecules and also in nodule development. Reddy et al. (2007) have recently reviewed the role of flavonoids in nodule initiation and development; this topic will be explored in further in Chapter 5.

3.4 Why was nodulation necessary?

A true mutualism, such as effective legume nodulation, brings benefits to both partners. Here the benefits to plants and bacteria will be explored in turn. In a thoughtful and much-quoted paper, McKey (1994) argued that the key to legume evolution involved a high nitrogen life style. Where this could not be maintained by taking up soil nitrogen, legumes developed symbioses with fungi and bacteria (mycorrhizas and nodules). The high nitrogen life style enabled them to produce leaves rich in nitrogen, which they could afford to recycle, and to develop nitrogen-rich seeds. Supporting evidence came from various sources, including analysis of the nitrogen content of leaves from all three sub-families, where it was found to be similar in non-nodulating and nodulating species, as also found by Sprent et al. (1996) for Brazilian legumes from the Cerrado and nearby areas. At the time McKey's paper was written, legumes were still believed to have originated in the humid tropics. He argued that by producing leaves high in nitrogen, photosynthetic capacity was increased, allowing plants to grow rapidly in favourable conditions and survive unfavourable conditions such as drought and fire. These are very persuasive arguments, but they do not always hold up when plants from some environments are studied. In particular, many of the sclerophyllous nodulated legumes that are found in Australia have long-lived, nutrient-poor

leaves and tend to use carbon rather than nitrogen compounds for protection against herbivory (Orians & Milewski, 2007). In such conditions, it has been argued (Sprent, 2007) that acacias (sl) can afford to have nodules with a range of effectiveness, since water, rather than nitrogen is often the limiting factor for growth. Nodules on such plants may be of more benefit to the bacteria than to the host. By living inside a nodule, bacteria are protected from adverse soils conditions and also supplied, via roots, with essential nutrients from a larger volume of soil than they could access for themselves.

Sprent (2007) pointed out that the time at which nodulated legumes evolved was one of great environmental change. At about 55 Ma, there was an abrupt increase in temperature of 5 to 10°C over a wide range of latitudes together with a major release of methane and carbon dioxide from sea floor sediments (Bowen et al., 2004; Sluijs et al., 2007). These conditions could have led to a degree of nitrogen limitation for plant growth, favouring the evolution of nitrogen-fixing symbioses. At about the same time, at least in parts of the neotropics, the fossil record shows a transient increase in plant biodiversity (Jaramillo et al., 2006). Since the major groups of legumes also had their origin at this time, it would be interesting to know if some of the diversity that did not survive included less efficient forms of legume nodulation.

The possibility that primitive rhizobia evolved from parasitic forms was discussed above. An alternative scenario is that the first nodulating bacteria were photosynthetic bradyrhizobia, capable of infecting plants via wounds, such as those forming stem nodules on *Aeschynomene* (Sprent & Raven, 1992). Photosynthetic ability was not needed when nodules formed underground, but some bradyrhizobia still retain the key enzyme, rubisco. Since these various arguments were put forward, the two genera *Rhizobium* (close to *Agrobacterium*) and *Bradyrhizobium* have been shown to belong to different families (Chapter 4). However, when these families separated is not known, so the bacterial side of nodule evolution, as well as the host plant side, currently has many unanswered questions. The whole position in the bacteria is complicated by the ability of many to exchange genetic material, a point that will be raised again in Chapter 4. For example, the wide host range strain NGR 234 contains genes with a high level of similarity to those of *Agrobacterium tumefaciens, Bradyrhizobium japonicum, Mesorhizobium loti* and the plant pathogen *Erwinia carotovora* (Streit et al., 2004).

3.5 Model legumes

In order to analyse the various stages of nodulation and nitrogen fixation in legumes, two species have been chosen as models, *Lotus japonicus* and *Medicago truncatula* (commonly known as barrel medic). These species have small genomes, small seed size (enabling them to be grown in bulk in test tubes) and endosymbionts whose genomes have been sequenced. In addition, they have determinate (*Lotus*) or indeterminate (*Medicago*) nodules. Using these species, a great deal of information about nodule development has been acquired, some of which will be dealt with in more detail in Chapter 5. The endosymbiont in use for *M. truncatula* is *Sinorhizobium meliloti* 1021, widely used as an inoculant for *M. sativa* (lucerne, alfalfa). Unfortunately the effectiveness of this host/rhizobial combination was not checked and it has now been shown

not to be fully effective in fixing nitrogen. Terpolilli et al. (2008) compared a number of species of *Medicago* and endosymbionts and concluded that *Sinorhizobium medicae* strain WSM 419, in use in Australia as a commercial inoculant for barrel medic, is fully effective with this host. As this strain has also now been sequenced, it is hoped that it will be used in future in preference to *S. meliloti*. To date there is no reason to question the effectiveness of *L. japonicus* with *Mesorhizobium loti* MAFF 303099, but like *Sinorhizobium meliloti* and *Medicago*, it is known to infect several *Lotus* species.

Another legume that has been promoted as a model is *Phaseolus vulgaris*. Its genome is not much larger than that of the two model legumes described above and it has the great advantage of being a very significant food source for many of the world's poorer peoples, especially in South America and Africa. Its disadvantages are its large seed size and the fact that it nodulates with a wide range of rhizobia. This may be one reason why nodulation is often poor. In spite of these disadvantages, Broughton et al. (2003) make a very good case for the study of this species as a model food legume, and to assist this they set up an international consortium named 'Phaseomics'. The consortium is looking at all of the many problems of this crop, including pests and diseases, as well as nodulation. Finally, *Pisum sativum*, the plant that helped launch the study of genetics, is still the subject of much research, including the most detailed description of the exchange of amino acids that is used to ensure a high degree of nodule effectiveness (Lodwig et al., 2003; Chapter 5).

The four species discussed so far, although from different tribes of legumes, all have a root hair infection pathway. Two important grain legumes with non-hair infection are lupins and peanuts (groundnuts). There are good arguments for a more detailed study of these, not only as crops in their own right, but also because a better understanding of their nodulation processes might be more relevant to the aim of extending nodulation ability to non-legumes. Gepts et al. (2005) reported on a meeting that drew up a plan for studying a wider range of legumes 'for food and feed'. This programme includes both peanut and *Phaseolus* and (of course) soybean. Is there a case for including non-papilionoid legumes? If the remit is extended beyond feeding humans, there certainly is, as genera such as *Acacia* are vital browse plants for both domestic and wild animals in much of Africa. Also the caesalpinioid species *Chamaecrista rotundifolia* is widely used in some parts of the tropics as a forage plant.

Since beginning this book, a major effort has been started to look at nodulation and other characteristics of *Chamaecrista fasciculata*, as a model for caesalpinioid legumes. This species, known in the United States as partridge pea, is a fairly small herb and easily grown. At a special session before the Fourth International Conference on Legume Genetics and Genomics in Mexico, December 2008, several groups outlined their plans for studying this species and significant new data may be expected soon. One intriguing paper has already emerged, giving the structure of a nodule haemoglobin. Gopalasubramaniam et al. (2008) found that this was intermediate in form between non-symbiotic haemoglobin and leghaemoglobin. This intermediate structure was predicted also to have intermediate oxygen-carrying properties, which could mean that its role in facilitating oxygen diffusion (see Section 5.7) is less important than for the papilionoid legumes that have so far been studied (Minchin et al., 2008). This raises several interesting questions, such as the efficiency with which *Ch. fasciculata* nodules fix nitrogen, There are no data making direct comparisons between nitrogen fixation by caesalpinioid legumes and by members of the other sub-families.

Chapter 4

Bacteria Nodulating Legumes

Early on in the study of bacteria nodulating legumes, it was realised that they were not all the same. Two categories were identified, fast-growing and slow-growing, and these were subsequently called *Rhizobium* and *Bradyrhizobium*, respectively (Jordan, 1982). Further differences include production of acid or alkali, respectively, when grown on suitable media and location of the nodulation (*nod*) and nitrogen-fixing (*nif*) genes. In *Rhizobium* and *Sinorhizobium* these are located on extrachromosomal DNA (plasmids), in *Bradyrhizobium* are chromosomal and in *Mesorhizobium* are on symbiotic islands located within the chromosome (see Section 4.6). There are many other differences between genera and species, such as preferred carbon substrates, salt tolerance and antibiotic tolerance. These features form part of the specific descriptions and can be found in the relevant references.

All the bacteria that are known to nodulate legumes are in the gram-negative Proteobacteria. This group is divided into five sections, coded by Greek letters. Only the α- and β-groups have members proven to nodulate legumes. Reports from the γ-group have not been authenticated and may represent casual nodule occupancy, a problem discussed later. The α-Proteobacteria contain seven orders, with all of the known nodulating genera being in Rhizobiales. Of the eleven families within this order, six are currently known to contain nodulating species. In some genera, e.g. *Bradyrhizobium*, all species are able to induce nodulation, but in others, e.g. *Phyllobacterium*, nodulating ability is restricted to one or a few species. The nomenclatural situation is further complicated by the suggestion that the largely plant-pathogenic genus *Agrobacterium* should be incorporated into *Rhizobium*. Farrand et al. (2003) discuss this and argue the case for retaining *Agrobacterium* as a separate genus, and this position is adopted here. On the basis of analysis of its *nodC* gene, a strain of *Bosea* (Bradyrhizobiaceae), isolated from nodules in Spanish gypsum-rich soils, is thought to nodulate various papilionoid legumes (Rincón et al., 2008). The β-Proteobacteria contain six orders, with all of the known nodulating members being in Burkholderiales, and within this order, in family Burkholderiaceae. Further details of bacterial taxonomy can be found in Garrity et al. (2004). This publication is revised regularly, but the current edition is

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out-of-date with respect to several recently reported species of nodulating bacteria, discussed below.

4.1 α-Proteobacteria

Table 4.1 lists the families and genera of α-Proteobacteria with nodulating species. *Ensifer* is considered in Garrity et al. (2004) as a genus separate from *Sinorhizobium*, but this issue is still subject to intense discussion. On balance, Martens et al. (2007), did not think the evidence for separation was yet sufficiently strong, but in 2008 they appear to have changed their minds (Martens et al., 2008). Certainly new species are being described under *Ensifer* (e.g. *E. mexicanus*, Lloret et al., 2007). In his comprehensive review of rhizobial ecology, Graham (2008) includes only one species under *Ensifer, E. adhaerens*, but note that this species is also considered by some to be *Sinorhizobium*. Graham's review also gives citations for all species of rhizobia, from both α- and β-Proteobacteria, and readers are referred to this work, except where species have been described more recently. As Graham (2008) points out, "additions to this list ... occur almost weekly" and several have been published during the writing of this book. Most of these are reported in the *International Journal of Systematic and Evolutionary Microbiology*, and readers who wish to keep up-to-date are advised to check this journal on line, as accepted papers are cited ahead of publication. The following sections will consider individual genera and the hosts of the various species, in the order in which the genera are listed in Table 4.1. In Tables 4.2 to 4.5 the rather small number of legumes involved represents the way in which research has proceeded. In general, people work on one or a few host species and identify the bacteria obtained from their nodules. Compared with the total number of nodulated legumes this covers only a very small minority of host plants.

By the time this volume is published there are likely to be more genera and species of nodulating bacteria described, for example an as-yet-unnamed pink-pigmented genus nodulating *Lotononis angolensis* (Yates et al., 2007).

Table 4.1 Genera in the families of Rhizobiales with known nodulating members *Ensifer* and *Sinorhizobium* added together under *Sinorhizobium*

Family	Genus	Species	Comments
Rhizobiaceae	*Rhizobium*	20	Several spp. have 2 or 3 biovars Includes *Allorhizobium*
	Sinorhizobium	13	
	Shinella	1	Not fully authenticated
Bradyrhizobiaceae	*Bradyrhizobium*	8	Includes *Blastobacter*
Hyphomicrobiaceae	*Azorhizobium*	2	
	Devosia	1	
Methylobacteriaceae	*Methylobacterium*	2	
Brucellaceae	*Ochrobactrum*	3	
Phyllobacteriaceae	*Mesorhizobium*	16	
	Phyllobacterium	1–2	

Table 4.2 Host plants known to be nodulated by species of *Rhizobium*. Specific names are given where these may indicate a degree of host specificity. *Macroptilium* refers to the broad host range 'trap' plant *M. atropurpureum*. Mimosoid hosts in bold type

Species	Biovar	Hosts
alkalisola[1]		*Caragana microphylla, Phaseolus vulgaris, Vigna radiata*
cellulosilyticum[2]		*Medicago sativa* (ineffective)
etli	*mimosae*	***Mimosa affinis*** and other ***Mimosa*** spp.[3]
	phaseoli	*P. vulgaris*
fabae[4]		*Vicia faba*
galegae	*officinalis*	*Galega officinalis*
	orientalis	*G. orientalis*
gallicum		***Leucaena**, Macroptilium, Onobrychis, P. vulgaris*
giardinii		***Desmanthus, Leucaena**, Macroptilium, P. vulgaris*
hainanense		*Arachis, Centrosema, Desmodium, Stylosanthes, Vigna*
huautlense		*Sesbania herbacea*
indigoferae		*Indigofera*
leguminosarum	*phaseoli*	*P. vulgaris*
	trifolii	*Trifolium*
	viciae	*Lathyrus, Lens, Pisum, Vicia*
loessense		*Astragalus, Lespedeza*
lusitanum[5]		*Phaseolus vulgaris*
mesosinicum[6]		*??????????????*
miluonense[7]		*Lespedeza chinensis*
multihospitium[8]		*Halimodendron halodendron, Robinia pseudoacacia*
mongolense		*Medicago ruthenica, P. vulgaris*
sullae		*Hedysarum coronarium*
tropici		*Dalea,**Leucaena**, Macroptilium,Onobrychis, P. vulgaris*
undicola[9]		***Acacia, Faidherbia**, Lotus, **Neptunia natans***
yanglingense		*Amphicarpaea, Coronilla, Gueldenstaedtia*

[1] Lu et al. (2009b).
[2] Garcia-Fraile et al. (2007).
[3] Elliott et al. (2008).
[4] Tian et al. (2009).
[5] Valverde et al. (2006).
[6] Lin et al. (2009).
[7] Gu et al. (2008).
[8] Han et al. (2008).
[9] Originally named *Allorhizobium undicola*.

4.1.1 Rhizobium

Currently recognised species and biovars are listed in Table 4.2. *R. gallicum* is sometimes split into biovars and *R. tropici* has a number of distinct groups. The species vary greatly in their host ranges, with *R. galegae* being the most restricted. While most of the hosts are from the Papilionoideae, *R. undicola* has more records of nodulation from Mimosoideae.

Further, most of the records for *Rhizobium* so far are from temperate areas. However, this situation will certainly change as more studies are carried out on tropical areas and harsh environments, such as dryland Africa. Also there is now great activity in parts of China, including the dry mountainous plateau regions, that is yielding much new information. For example, Kan et al. (2007) found that species of *Oxytropis* and *Medicago archiducis-nicolai* could be nodulated by *R. leguminosarum*. On the other hand, in subtropical regions of China, Liu et al. (2007) found that *Trifolium pratense* and *T. repens*, which are normally nodulated by *R. leguminosarum* bv *trifolii*, could form nodules with strains belonging to *Bradyrhizobium, Mesorhizobium* and *Sinorhizobium. R. multihospitium* was so named because of the large number of species in Xinjiang province, China, from which it was isolated (Han et al., 2008). So far it has only been shown to nodulate effectively the two species given in Table 4.2, but Han et al. (2008) note that the legumes from which the species was isolated grow in alkaline soils with high salt concentrations, so conditions used in their experiments may not have been optimal. Minor differences in growth conditions can make the difference between formation of ineffective or effective nodules, as we have found when growing *Mimosa* species and other tropical legumes in sub-optimal light conditions (E.K. James, personal communication). *R. cellulosilyticum* is included in Table 4.2, even though it has only been shown to form ineffective nodules on *Medicago sativa* (Garcia-Fraile et al., 2007), because of its genetic constitution. However, until it has been shown to form effective nodules on a legume, its nodulation status should be regarded with caution. There is a proposal to rename the widely studied *R. leguminosarum*, *R. pisi* (Ramírez-Bahena et al., 2008). The proliferation of taxa has been questioned by some microbiologists who take a more evolutionary view of rhizobia. For example, Silva et al. (2005) looked at the genetic structure of *R. gallicum* and related species, studying both chromosomal and plasmid genes as well as their biogeography. They concluded that *R. mongolense* and *R. yanglingense* belong to the evolutionary lineage of *R. gallicum* and should be reclassified as biovar *orientale* of that species. Plant taxonomists have long been divided into 'lumpers' and 'splitters', and rhizobial taxonomists may be going the same way!

4.1.2 Sinorhizobium *and* Ensifer

Sinorhizobium and *Ensifer* are grouped together in Table 4.3. As with *Rhizobium*, most of the hosts are papilionoid, but with a significant number of mimosoids. The model legume *Medicago truncatula* can be nodulated by several sinorhizobia, but recent work has shown that the species used in the model system, *Sinorhizobium meliloti*, is not very good at fixing nitrogen with this host, preferring to associate with *M. sativa* (see above). The fast-growing, wide host range NGR 234 may be conspecific with *S. fredii* or a separate species of *Sinorhizobium*. Either way it is unique in the number of genera and species with which it can nodulate (Pueppke & Broughton, 1999). *S. adhaerens* is a soil bacterium that can adhere to (hence the specific name) and lyse other soil bacteria. As yet there is no really clear evidence that it can nodulate any species of legume (hence the ?? in Table 4.3), but it has been suggested that it might acquire nodulation genes from other rhizobia (Willems et al., 2003).

Table 4.3 Host plants known to be nodulated by species of *Sinorhizobium/Ensifer*. Mimosoid genera indicated in bold

Species	Hosts
abri	*Abrus precatorius*
adhaerens	*????*
arboris	***Acacia senegal, Prosopis chilensis***
fredii	*Glycine max*
indiaense	*Sesbania rostrata*
kostiense	***Acacia senegal, Prosopis chilensis***
kummerowiae	*Kummerowia stipulacea*
medicae	*Medicago orbicula, M. polymorpha, M. truncatula*
meliloti	*Medicago. Melilotus, Trigonella*
mexicanus[1]	***Acacia angustissima***
morelense	***Leucaena leucocephala***
saheli	***Acacia***, *Sesbania*
terangae	***Acacia***, *Sesbania*
xinjiangense[2]	*Glycine max*

[1] Lloret et al. (2007). This host species has now been placed in the genus *Acaciella* (see Chapter 1).
[2] Now thought to be conspecific with *S. fredii* (Martens et al., 2008).

4.1.3 Other members of Rhizobiaceae

Another genus in the Rhizobiaceae, *Shinella*, has recently been isolated from the important Chinese herb species *Kummerowia stipulacea* (Lin et al., 2008). Although this isolate was not fully authenticated by showing nodulation on its host of origin, the fact that it possesses *nodCD* genes and *nifH* similar to those in *Rhizobium etli* supports its inclusion as a genuine nodulating organism.

4.1.4 Bradyrhizobium

Table 4.4 gives the currently accepted species of *Bradyrhizobium*. Most are from soybeans and none as yet from outside Papilionoideae. As noted above for *Trifolium*,

Table 4.4 Host plants known to be nodulated by species of *Bradyrhizobium*

Species	Hosts
canariense	*Chamaecytisus, Lupinus*
denitrificans	*Aeschynomene indica*
elkani	*Glycine max*
japonicum	*Glycine max*
jicomae[1]	*Pachyrhizus erosus*
liaoningense	*Glycine max*
pachyrhizi[1]	*Pachyrhizus erosus*
yuanmingense	*Lespedeza, Medicago, Melilotus*

[1] Ramirez-Bahena et al. (2009).

bradyrhizobia are reported in Table 4.3 that nodulate the related genera *Medicago*, and *Melilotus*. *B. denitrificans* was originally called *Blastobacter denitrificans*. There are still many difficulties with this genus and several species are loosely defined as, for example, *Bradyrhizobium* sp. (*Lupinus*). This is a particularly interesting species as it comes from Mediterranean areas, where bradyrhizobia are uncommon, and is both acid and aluminium tolerant (Howieson et al., 1998). There are also a number of photosynthetic bradyrhizobia, not yet categorised at the specific level, but with numerous interesting features. Some of them lack the common nod genes *nodABC*, essential for root hair infection; these can nodulate some species of *Aeschynomene*, by a crack entry process (Giraud et al., 2007). The genus *Aeschynomene* has at least 180 species of which 41 are known to nodulate (Table 1.9). Most of these have been further divided according to whether or not they form stem nodules and, more recently, whether the latter nodulate with photosynthetic bradyrhizobia. The three resulting groups are I, those that do not form stem nodules, their root nodules being initiated by strains of the so-called cowpea miscellany of bradyrhizobia; II, stem-nodulating species that can nodulate with either photosynthetic or non-photosynthetic bradyrhizobia; and III, those nodulated exclusively by photosynthetic bradyrhizobia. (Giraud & Fleischman, 2004). The stem-nodulating species have been further sub-divided according to conditions under which nodules are formed (Boivin et al., 1997; see also Section 5.5.1). In evolutionary terms, there is the possibility that the primitive state of bradyrhizobia was photosynthetic and root-nodulating forms have lost this ability. The ability to photosynthesise could be a particular advantage in the free-living state of the bacteria, when they are found on the surfaces of leaves and stems. A further interesting feature of at least one of these strains, *Bradyrhizobium* sp. ORS278, is that it appears to have acquired a bacteriophytochrome gene by lateral transfer, probably from a cyanobacterium (Jaubert et al., 2007). With this suite of light-sensing genes, strain ORS278 seems well equipped for both free and symbiotic life. In addition to the defined species there are many other bradyrhizobia reported to nodulate all three sub-families of legumes (see examples in Chapter 1).

4.1.5 Azorhizobium *and* Devosia

Both *Azorhizobium* and *Devosia* are in family Hyphomicrobiaceae. *A. caulinodans* was first described in 1988 and aroused great interest for a variety of reasons, one of which was its ability to fix nitrogen and grow on the products ex planta. It is also the symbiont of *Sesbania rostrata* (see Chapters 1, 3 and 5), which has been the subject of a great deal of research. As mentioned earlier, although it forms nodules on the stem of its host, these are not stem nodules in the strict sense as they are plumbed into adventitious root initials. More recently a second species, *A. doebereinerae*, has been described, this time from the root nodules of of *Sesbania virgata*. This species of *Azorhizobium* has only low nitrogenase activity ex planta (Moreira et al., (2006). Both species show a high degree of specificity for their hosts. The genome of *A. caulinodans* has now been sequenced. It is closely related to species of *Xanthobacter* that can fix nitrogen in the free-living state, and it was suggested that the capacity for *A. caulinodans* to nodulate was probably acquired by horizontal transfer of a symbiotic island, from an as-yet-unknown ancestor (Lee et al., 2008). *Devosia* has two species, but only *D. neptuniae*, from *Neptunia natans*, an aquatic mimosoid legume from India, has been shown to fix nitrogen (Rivas et al., 2003).

4.1.6 Methylobacterium

M. nodulans was first described from nodules of species of *Crotalaria* (Sy et al., 2001). One of its characteristics was the ability to metabolise methanol, but another species, not yet fully characterised, nodulating some *Lotononis* species, does not (Yates et al., 2007). Renier et al. (2008) examined in more detail the interactions between *M. nodulans* ORS2060 and *C. podocarpa*. They found that these two symbionts interacted in a generally similar way to other host/rhizobia pairs, with difference in detail, such as structure of Nod factors. They further suggested, as for *Azorhizobium* (above) and *Phyllobacterium* (see Section 4.1.9), that *nod* genes have been acquired by lateral transfer from other, as yet unidentified rhizobia.

4.1.7 Ochrobactrum

The genus *Ochrobactrum* is classified in family Brucellaceae, which also includes the important animal and human pathogenic genus *Brucella*. There are interesting similarities between these pathogens and nodulating bacteria, which have been discussed elsewhere (Batut et al., 2004; Soto et al., 2006).

There are now three reports that species of *Ochrobactrum* nodulate legumes. The first was from Ngom et al. (2004), who isolated an as-yet-unnamed species from nodules of *Acacia mangium* grown in the Philippines and Thailand. This strain was able to form effective nodules on *A. mangium*, *Faidherbia albida* (cited as *A. albida*) and *Falcataria moluccana* (cited as *Paraserianthes falcataria*), all mimosoid legumes. The second report was of *O. lupini*, isolated from *Lupinus honoratus* in Argentina and able to nodulate *L. albus* (Trujillo et al., 2005). The nodules were formed in the axils of lateral roots, rather than along the root as is usual for lupin (Chapters 1 and 3), but, on the basis of plant weight, were found to be effective. No structural details were given. The third report was of *O. cytisi*, isolated from nodules of *Cytisus scoparius* in Spain and found to form ineffective nodules on *Phaseolus vulgaris*, but not tested on its host of isolation (Zurdo-Piñeiro et al., 2007). Thus we have an interesting but frustrating situation in which two or three species of *Ochrobactrum*, isolated from three continents, appear to be able to nodulate mimosoid and papilionoid legumes via root hairs, forming indeterminate (mimosoid species) and determinate (*P. vulgaris*) nodules as well as non–hair-infected nodules (lupins and possibly *Cytisus*).

4.1.8 Mesorhizobium

Classified in the Phyllobacteriaceae, *Mesorhizobium* is a genus nodulating a wide variety of legumes, including several mimosoid genera and a caesalpiniod one (*Chamaecrista*). It is worth noting that the latter genus can also be nodulated by the widely used inoculant strain CB756, a member of the cowpea miscellany in the bradyrhizobia. Table 4.5 lists the currently described species. Note that there are three additions to the references cited in Graham (2008) – the book containing this chapter had rather a long gestation time! There are likely to be further additions shortly, since, for example, Donate-Correa et al. (2007) isolated a range of mesorhizobia from *Anagyris latifolia* in the Canary Islands and thought some of these would be identified as new species.

Table 4.5 Currently described species of *Mesorhizobium* and their hosts. Mimosoid genera in bold and caesalpiniod in Roman type

Species	Biovar	Hosts
albiziae[1]		***Albizia***, *Glycine max*, ***Leucaena***, *P. vulgaris*
amorphae		*Amorpha fruticosa*
australicum[2]		*Biserrula pelecinus, Astragalus membranaceus*
caraganae[3]		*Astragalus, Caragana, Glycyrrhiza, P. vulgaris*
chacoense		***Prosopis alba***
ciceri		*Cicer arietinum*
	biserrulae[4]	*Biserrula pelecinus*
huakuii		***Acacia***, *Astragalus*
loti		*Lotus*
mediterraneum		*Cicer arietinum*
metallidurans[5]		*Anthyllis vulnararia*
opportunistum[2]		*Biserrula pelecinus, Astragalus* spp. *Lotus peregrinus*
plurifarum		***Acacia***, Chamaecrista, ***Prosopis, Leucaena***
septentrionale		*Astragalus adsurgens*
shangrilense[6]		*Caragana, Vigna, P. vulgaris*
temperatum		*Astragalus adsurgens*
tianshanense		*Caragena, Glycine, Glycyrrhiza, Sophora*

[1] Wang et al. (2007).
[2] Nandasena et al. (2009).
[3] Guan et al. (2008).
[4] Nandasena et al. (2007).
[5] Vidal et al. (2009).
[6] Lu et al. (2009).

In this work, it was suggested that lateral transfer of *nod* genes had occurred. Lateral transfer was also found in *M. cicerae* bv *biserrulae*, by Nandasene et al. (2006), where inoculated strains exchanged symbiotic islands with rhizobia in soil, leading to rapid loss of effectiveness. The complete gene sequence of a strain of *M. loti* that is used in the study of symbiosis in the model legume *Lotus japonicus* has been sequenced (Kaneko et al., 2000).

4.1.9 Phyllobacterium

Phyllobacterium is a relative newcomer to the nodulation scene. In 2005 Valverde et al. isolated a species that they called *P. trifolii*, from Spanish soils, and showed that it could nodulate both *Trifolium repens* and *Lupinus albus*. Baimiev et al. (2007) isolated a strain closely related to *P. trifolii* from nodules of Hungarian sainfoin (a species of *Onobrychis*), but it is not clear whether or not it could nodulate this host. Mahdi et al. (2007) isolated phyllobacteria from nodules of *Genista saharae* in Tunisian soils, but found that these isolates could not nodulate the host of isolation. *Phyllobacterium*-like bacteria were isolated from *Ononis tridentata* in a range of Spanish soils (Rincón et al., 2008), so we may expect further confirmed nodulation reports from this genus to emerge.

4.2 β-Proteobacteria

Table 4.6 lists the species of β-Proteobacteria (collectively known as β-rhizobia) currently known to nodulate and fix nitrogen in legumes. As with the α-Proteobacteria there is a strong relation between nodulating species and pathogens. Indeed, the first species to be properly identified (*Cupriavidus taiwanensis*, then called *Ralstonia taiwanensis*; Chen et al., 2001) was isolated not only from nodules but also from sputum of patients with cystic fibrosis. *Burkholderia* has species that are plant and animal pathogens as well as legume symbionts, soil heterotrophs and strains that can fix nitrogen in association with grasses and other plants (Estrada de Los Santos et al., 2001). In addition to the species in Table 4.6 there are numerous other reports of *Burkholderia* strains able to nodulate legumes, and several of these are likely to be designated as new species in due course – for example, strains isolated from a South African *Rhynchosia* species (Garau et al., 2009). *B. cepacia* is a complex species with many pathogenic strains and which has also been isolated from nodules (Rasolomampianina et al., 2005). This species has recently been divided into five (Vanlaere et al., 2008). Burkholderias have also been found to nodulate *Lebeckia* (J.G. Howieson, personal communication). Some species, like some α-rhizobia, can also fix nitrogen ex planta and grow on the products (Elliott et al., 2007a).

The most detailed studies of the infection and development of nodules induced by *Burkholderia* species are those on species of *Mimosa* and *Cyclopia* (Elliott et al., 2007a, b). Both of these genera have a hair infection and form indeterminate nodules. However, the results of Rasolomampian et al. (2005) with *Dalbergia* (crack infection, no infection threads, determinate nodules) and Garau et al. (2008) with *Rhynchosia* (hair

Table 4.6 Nodulation of legumes by defined species of β-rhizobia. Several other species are likely to be published soon (see text). *B., Burkholderia*; *C., Cupriavidus*, *M., Mimosa*

Species	Origin of type strain	Characteristics	Reference
B. mimosarum	*M. pigra* in Taiwan	Highly competitive for nodulation of invasive *Mimosa* spp.	Chen et al. (2006)
B. nodosa	*M. scabrella* in Brazil	Not yet found outside Brazil	Chen et al. (2007)
B. phymatum	*Machaerium lunatum*[1]	Broad host range in Mimosoideae. Fixes N_2 ex planta	Moulin et al. (2001); Vandamme et al. (2002); Elliott et al. (2007a)
B. sabiae	*M. caesalpinifolia*	No other hosts known	Chen et al. (2008)
B. tuberum	*Aspalathus carnosa*[1]	Nodulates *Cyclopia* spp. but not several *Aspalathus* spp. Fixes N_2 ex planta	Moulin et al. (2001); Vandamme et al. (2002); Elliott et al. (2007b)
C. taiwanensis	*M. pudica* in Taiwan	Broad host range for *Mimosa* spp.	Chen et al. (2001) Elliott et al. (2007a)

[1] Not authenticated on host of isolation, and in the case of *Machaerium*, roots possibly mistaken for those of a *Mimosa* species.

infection, determinate nodules) suggest that burkholderias can infect legumes and induce nodulation in all the ways shown for classical rhizobia. Further, plants nodulated by β-rhizobia may be herbaceous, shrubby, trees, annual or perennial. At the moment all reports are from tropical or warm temperate areas and information to date indicates that β-rhizobia have acquired *nod* genes from local α-rhizobia (e.g. Elliott et al., 2007a). There may be considerable geographical variation in the occurrence of *Burkholderia* species in nodules. For example, Parker (2008) looked at bacteria in nodules of 24 species from 18 legume genera, including all sub-families, in Barro Colorado Island, Panama and found the majority to be bradyrhizobia, with the next most abundant being *Burkholderia*, but the latter were only found in plants from Mimosoideae. There may also be within genus variation, for example in the papilionoid *Lebeckia*, where most species nodulate with a variety of α-rhizobia, but those from section Lebeckia may be nodulated by *Burkholderia* (Phallane et al., 2008)

4.3 Other bacterial nodule occupants

Nodules may house various bacteria, not all of which are able either to fix nitrogen or to induce nodules. It is not sufficient to isolate a bacterium from a nodule and assume that it can nodulate the host of isolation, a fact that has led to a number of unfortunate errors in recent publications, even in prestigious journals such as *Nature* (e.g. Moulin et al., 2001). In one case the bacteria were from a nodulating strain, but not for the plant from which it was allegedly isolated. It is essential that Koch's postulates be established before claims are made, particularly if the bacteria concerned are not known to be nodulating forms. Benhizia et al. (2004) isolated several genera of γ-Proteobacteria from nodules of *Hedysarum* species and implied that these could nodulate their hosts of isolation (indeed the title of the paper said so), but no evidence of this was given, and in a later paper they found that these γ-Proteobacteria were unable to nodulate their hosts (Muresu et al., 2008). These workers had a particularly difficult situation in that the rhizobia in their active nodules were very difficult to culture. Chou et al. (2007) isolated a new species of the γ-Proteobacterial genus *Labrys*, *L. neptuniae*, from nodules of *Neptunia oleracea*, but showed that this bacterium could not nodulate its host of isolation. To date, there is no good evidence that γ-Proteobacteria can nodulate legumes. On the other hand, non-nodulating bacteria from various genera are frequently isolated from nodules. In a detailed study of bacteria isolated from soybean nodules in China, 98 strains of non-nodulating forms from the α, β, and γ-Proteobacteria were found (Li et al., 2008). Some of these could produce indole acetic acid, could solubilise mineral phosphate and fix nitrogen, with their *nifH* genes being very similar to those of the nodulating bacterium *Bradyrhizobium japonicum*. Although these non-nodulating bacteria had the potential to aid plant growth, Li et al. (2008) were unable to obtain evidence that they actually did so. These and other studies, not cited, give very strong evidence that legume root nodules may contain a range of bacteria that are unable to nodulate their hosts. How they get into the nodules, and what, if anything, they do there (apart from having a nice culture medium to live in), is not clear. Whether they are more common in wild legumes than cultivated ones, as

suggested by Muresu et al. (2008), needs further investigation, as does the possibility that a high level of non-nodulating bacteria may be associated with nonculturable rhizobia. Judging by the work of Li et al. (2008) this is not always the case.

4.4 Specificity

Specificity is another area where things are changing rapidly and, again, this is largely due to the fact that more work is now being done on legumes outside the narrow confines of temperate agriculture. However, the most detailed work on the recognition between host and symbiont is still being carried out on temperate species, in particular the model legumes *Medicago truncatula* and *Lotus japonicus* (see Chapters 3 and 5). The most stringent conditions are when there is a gene for gene 'pairing' between the host and bacterium. So far such a high level of specificity has only been demonstrated for temperate papilionoid legumes. The early work of Nutman (1969) on species of clover was followed by the discovery that a variety of pea from markets in Iran, subsequently referred to as *Pisum sativum* cv Afghanistan, could not nodulate with the standard rhizobia used in European agriculture (Lie et al., 1976). More recent studies are unravelling the molecular bases for these differences (e.g. Firmin et al., 1993, for peas; and Roddam et al., 2002, for subterranean clover).

In order to form nodules, a series of molecular exchanges between the host plant and bacteria is involved. Of the various types of compound produced by the host plant, phenolic compounds, especially flavonoids, have been the most widely studied. These are secreted by roots of many plants, apparently being an ancient characteristic. However, legumes use this general class of compounds to communicate with rhizobia and stimulate the production of Nod factors. Nodulation genes and Nod factors have been extensively studied and described. Unfortunately not everyone uses the same terminology, which makes it difficult for the non-expert to follow the trail from soil to functional nodules. In this section the early stages of interaction involving specificity will be summarised. Chapter 5 will deal with later interactions that lead to various nodule types and levels of effectiveness.

All nodulating bacteria that have been studied have the common nodulation gene *nodD* that, in the presence of suitable flavonoids, leads to the production of NodD proteins. These in turn interact with one or more *nod* boxes, leading to the production of Nod factors that are implicated in specificity (Kobayashi & Broughton, 2008). One *nod* box consists of the common nodulation genes, *nodABCIJ*. The first three of these are concerned with the production of Nod factors and the last two their secretion. It was noted earlier that some photosynthetic bradyrhizobia lack *nodABC*, whose function has only been proven for the root hair infection pathway. The common feature of all *nodABC* products is the synthesis of a backbone of β 1-4 linked *N*-acteylglucosamine residues, similar to the chitin molecules found in insect exoskeletons and fungal cell walls (Fig. 4.1). This backbone is decorated at various points with fatty acid and other residues that are involved in host specificity and in the type of nodule formed (determinate or indeterminate); see the review by D'Haeze and Holsters (2002). In general, the more different decorations a strain can produce, the more host species it can nodulate, the record

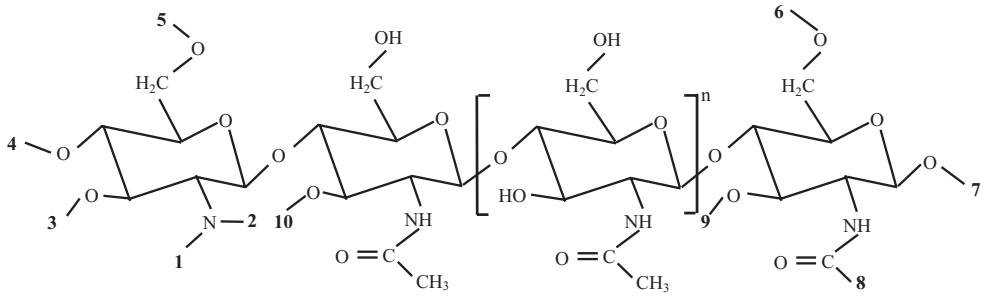

Figure 4.1 Basic features of lipochitin-oligosaccharides, or Nod-factors. They all have a backbone of β1.4 linked *N*-acetyl glucosamine, with a varying number of residues. In the figure, n = 0–3. The backbone is decorated with up to 10 groups of varying complexity. The list gives the main ones included in the review of D'Haeze & Holsters (2002). For a recent account of the synthesis of Nod factors, see Kobayashi & Broughton (2008). Positions 1 and 6 are especially critical for nodule type (determinate or indeterminate) and specificity, respectively. (1, fatty acyl chains of C14–C20, with varying degrees of unsaturation; 2, Me or H; 3, 4, 5, carbamoyl, acteyl or H; 6, fucosyl, arabinosyl. sulphate or H; 7, usually H, rarely mannosyl or glycerol; 8, usually Me, sometimes H; 9, usually H, sometimes arabinosyl or fucosyl; 10, usually H, rarely acetyl or fucosyl.)

being held by NGR234, an organism first isolated by Trinick in Papua New Guinea and since widely studied by Broughton's group in Geneva. In their 1999 paper, Pueppke and Broughton give a nice historical account of studies on specificity in general and on NGR234 in particular. They list hundreds of host legumes, from all three sub-families, that can be nodulated, not always effectively by this strain. However, most of these hosts are tropical or subtropical and there are some interesting anomalies; for example, Australian acacias are generally nodulated by NGR234, but African ones are not.

Variation in specificity within species has been noted above for *P. sativum*. This situation is not uncommon in legume species that have been domesticated for many years, as is well illustrated by *P. vulgaris* (Graham, 2008). Graham notes that this species is nodulated by more than a dozen different rhizobia, from three genera (*Bradyrhizobium, Rhizobium, Sinorhizobium*) and yet shows some degree of specificity in different geographical regions. In its centre of origin in South America, *R. etli* is the major endophyte, whereas in parts of Europe, North Africa and the United States, *R. gallicum* is often used. Perhaps surprisingly, *R. leguminosarum* bv *phaseoli* is found less often, but is common in France and Tunisia. Further details of this and other examples can be found in Graham (2008). Cultivated *P. vulgaris* is less promiscuous in the number of rhizobia with which it nodulates than ancestral forms (Souza et al., 1994). This may be a general phenomenon in unimproved legumes from tropical areas, since many of the species studied have been shown to nodulate with a wide variety of rhizobia, for example, both African and Australian acacias, with widely different levels of effectiveness (Burdon et al., 1999; Nick, 1998; Odee et al., 2002; Thrall et al., 2000, 2007). However, this may also be true for temperate regions, as Mutch and Young (2004) found that wild species of legumes in eastern England were more promiscuous than crop species grown in the same soil in their ability to nodulate with strains of *R. leguminosarum* bv *viciae*.

Variations in species of bacteria nodulating different species within a host genus are common, as is shown in the examples given in Tables 4.2 to 4.6. This may extend to

species being nodulated by different genera of endophyte, as in the case of *Lotononis*, where some species are nodulated by *Methylobacterium nodulans* and others by an as-yet-unnamed species from the α-Proteobacteria (Yates et al., 2007). In *Lebeckia*, some species are nodulated by α- and others by β-Proteobacteria (Phallane et al., 2008).

4.5 Competition

If a host is grown in a soil that contains several strains of bacteria that can potentially nodulate it, who gets in? Do the numbers of bacteria in the rhizosphere play a part? Graham (2008) discusses the use of the term 'competitiveness' and concludes that it covers a variety of aspects of the relationship between the legume host and potential endophytes and suggests that it really means 'success in nodule occupancy'. Clearly this must include the more traditional features of competitiveness, such as ability to persist in the soil in the absence of a host, to grow actively in the rhizosphere and attach to host roots when the host is reintroduced. This further requires that the bacteria are in the correct position with respect to the host root. Thus in the early stages of growth, they need to be near the crown of the root system, but later they may need to be deeper in the soil. Further, the root architecture of the host and its phenology (vegetative or reproductive phases of growth) can influence rhizobial population structure, as shown for *Rhizobium leguminosarum* biovar *vicieae* around *Pisum sativum* plants (Depret & Laguerre, 2008). It is possible that different rhizobial genotypes may be better at producing effective nodules at different stages of host development. Graham (2008) stressed that it is necessary that a 'competitive' strain completes the infection events in a 'timely' manner. Ampomah et al. (2008) found that strains of *Sinorhizobium* that are unable to catabolise the sugar trehalose could produce more nodules on some host genotypes, even when they were poor colonisers, the accumulation of trehalose in the infecton threads apparently giving them an advantage.

Competitiveness is also affected by edaphic factors. Of these, pH, temperature, desiccation and nutrient status have been most widely studied. For example, acid-tolerant strains of *R. tropici* are more likely to be recovered from nodules grown in acid than neutral soils and fast-growing rhizobia from soybean nodules at alkaline pH (reviewed by Graham, 2008). Soil nutrients, both macro and micro, can affect rhizobia directly, as they have to live as saprophytes in the absence of host plants. Wielbo et al. (2007) found that within *R. leguminosarum*, strains that could use the widest range of nutrients, especially organic and amino acids, were the most competitive. In addition, soil factors may affect competition via effects on the host plant (Sadowski, 2005). Although combined nitrogen, usually in the form of nitrate or ammonium nitrate, has been widely found to inhibited nodulation, its mechanism of action on competition is not well understood. Because of the bias of research towards agricultural systems where nitrate is the predominant form of soil nitrogen, it is often not realised that many legumes can nodulate and fix nitrogen in the presence of ammonium, which is the predominant form of nitrogen in many natural soils and in most forests. In the mimosoid tree *Mimosa caesalpinifolia* and the papilionoid tree *Gliricida sepium*, respectively, nitrate inhibited nodulation, but ammonium at the same concentration

did not, and in the latter host nitrate reduced the proportion of plant nitrogen derived from fixation whereas ammonium did not. These and other data are reviewed in Sprent (1999). More recently Ruffel et al. (2008) have shown in *Medicago truncatula* that different nitrogen sources may affect different gene regulatory systems in different ways. In particular under conditions of low nitrogen supply, root systems up-regulated genes for nitrate uptake, but not those for ammonium uptake or nitrogen fixation. In some species of *Mimosa* that normally nodulate with β-rhizobia in the field in Brazil, but that can also accept α-rhizobia, the balance of competition between these two types of rhizobia is affected by nitrate and/or ammonium (Elliott et al., 2008).

4.6 Stability and genetic exchange

Most of the early work on rhizobial genetics was carried out on species of *Rhizobium* because the DNA for nodulation and nitrogen-fixing characteristics is located on plasmids, rather than on the chromosomes. Plasmids can be readily transferred between strains and even species (see the review by Farrand, 1998). Slow-growing rhizobia of the Bradyrhizobiaceae have both their 'housekeeping' genes and their nitrogen-fixing genes on chromosomes, making experimentation more difficult. However, Sullivan et al. (1995) found that *Mesorhizobium loti* (then called *Rhizobium loti*) had symbiotic islands in its chromosome, which could be transferred to other rhizobia in soil. Similar results have been found for *Mesorhizobium cicerae* biovar *biserrulae* (Nandasene et al., 2006). These differences are important for a number of reasons. In practical terms, lateral transfer of genes between rhizobia in soil causes problems for persistence of inoculant strains (Nandasene et al., 2006). It could also be of benefit to native and introduced legumes. For example, Chen et al. (2008) found that there appeared to be considerable lateral transfer amongst species of *Mesorhizobium*, enabling those that normally nodulate other genera (such as *M. tianshanense* for *Glycyrrhiza*) to nodulate species of *Caragana*. In the very inhospitable Tibet plateau, Hou et al. (2008) found extensive lateral transfer between rhizobial genera and concluded that this may be associated with the need for the bacteria to adapt to local extreme conditions. In a wide range of areas of temperate China, the large genus *Astragalus* was found to be nodulated with a wide variety of rhizobia, again with extensive lateral transfer among them (Zhou et al., 2008). On the other hand, Zhang et al. (2008) found that symbiotic genes in bradyrhizobia nodulating *Vigna* species in China were chiefly maintained by vertical, rather than horizontal (lateral) transfer. No good evidence from field studies has been found that shows lateral transfer in bradyrhizobia. So far, none of these extensive studies from China, nor others from temperate regions outside parts of South Africa, have reported any β-rhizobia nodulating native legumes.

In common with many bacteria, rhizobia function at a population level, for example in the process of quorum sensing, where a population can react metabolically to its environment (see Chapter 5). This is true of both α- and β-rhizobia (Oldroyd & Downie, 2008; Suárez-Moreno et al., 2008), and may have been an early evolutionary event (Diggle et al., 2007).

Chapter 5

Development and Functioning of Nodules

In order for nitrogen fixation by legume nodules to be fully effective, i.e. allowing plants to grow at least as well as they can on combined nitrogen, host and bacterial processes need to be closely integrated. How this may be achieved in some advanced papilionoid species will be considered first. Studies on these have centred on the model legumes, *Medicago truncatula* (Jones et al., 2007) and *Lotus japonicus* (Udvardi et al., 2005) and a few other species such as *Pisum sativum* and *Glycine max*. These are often thought to illustrate typical indeterminate (*Medicago, Pisum*) and determinate (*Lotus, Glycine*) nodules, respectively. Table 5.1 lists the major differences between these types of nodules. Initial infection in both types is similar and occurs through root hairs. As briefly mentioned earlier (Chapter 3), hair infection is preceded by the secretion of flavonoids and related substances by the host root. Not all of these will act as *nod* inducers in any or all legumes, and they may serve other purposes such as substrates for rhizobial growth (Cooper, 2004). The latter paper lists those flavonoids that are known to induce *nod* genes in various legumes. Dakora (2000) found considerable commonality among *nod* gene-inducing flavonoids from five members of legume tribe Phaseoleae. This and other evidence suggests that production of flavonoids may also have host taxonomic significance. In order for sufficient bacteria to reach the root surface a number of other processes are involved. These include motility and chemotaxis (Poole et al., 2008). When sufficient bacteria are present they may affect gene expression by a density-dependent phenomenon known as quorum sensing (reviewed by Poole et al., 2008, and recently shown by Suárez-Moreno et al., 2008, to be present also in *Burkholderia* spp.). Quorum sensing may be associated with biofilm formation, thought to be an ancestral process found in both α- and β-rhizobia and controlled by the common *nod* genes, *nodABCD1* (Fujishige et al., 2008) As mentioned in Chapter 4, *nodABC* genes code for the biosynthesis of the lipochitin oligosaccharide backbone of the Nod factor (Fig. 4.1). *NodEH* code for the decorations on the LPS backbone that lead to host specificity: wide host range strains have several of these genes. In *Azorhizobium caulinodans* some decorations are essential for root hair, but not crack infections (Oldroyd & Downie, 2008). Further components of the pre-infection stage are lectins on the root hairs, which aid rhizobial adhesion to the hairs and surface polysaccharides on the rhizobia. Whether the latter act as signal molecules or as a means of evading plant

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Table 5.1 Major differences between indeterminate and determinate nodules of advanced papilionoid legumes with a root hair infection. Where features differ between determinate nodules of the phaseoloid tribes and *Lotus* this is indicated

Feature	Indeterminate	Determinate	Reference
Initiation of cell division[1]	Inner cortex	Outer cortex[2]	Brewin (2004)
Meristematic growth	Apical, continuous	Limited	Sprent (2001)
Division of infected cells	No	Yes	
Life span	Potentially perennial	Limited	
Final shape of nodules	Cylindrical, often branched	Spherical, with lenticels	
Vascular transfer cells	Present in some	Absent	Pate et al. (1969)
Bacteroids in symbiosomes	Single, rods or (rarely) pleomorphic, large, increased DNA	Several, usually rod shaped	Mergaert et al.(2006)
Bacteroid viability	Absent	Present	Sprent (2001)
PHB[3] in bacteroids	Low or absent	Often high	Trainer & Charles (2006)
Export product	Amides	Ureides[4]	Sprent (2001)

[1] In *Lotus* it is middle cortex.
[2] May be controlled by auxin levels (Kondorosi et al., 2005).
[3] Poly β-hydroxybutyrate.
[4] Except in *Lotus* and other members of tribe Loteae with determinate nodules.

defence responses is not yet clear (Oldroyd & Downie, 2008). Nod factors are perceived by the host root epidermis, in the region of production of root hairs. Here they lead to induction of the early nodulation (*ENOD*) genes as well as oscillations in calcium levels in the cytosol of hairs (calcium spiking). Calcium spiking is the subject of intensive research and is a complex process involving root hair nuclei and eventually leading to transcription of *ENOD* genes. The current state-of play is discussed by Oldroyd and Downie (2008). The situation in legumes without root hair infection is unknown.

5.1 Root hair infection

The overall process of root hair infection is described in most elementary textbooks, having been known for over a century. However, the finer details of the process are only now being unravelled. The first problem is how do bacteria manage to breach the hair cell wall and enter against its turgor pressure? This has been excellently reviewed by Brewin (2004), with a short update in Brewin et al. (2008). The process appears to be very similar in all papilionoid legumes that have been studied in sufficient detail and there is no reason to suppose that it is different in recently described root hair infections by β-rhizobia in mimosoid nodules (Elliott et al., 2007a). It is initiated by Nod factors thought to be produced by rhizobia adhering to the hair, and the first response is that the root hair tip ceases to grow and usually becomes swollen. Growth is resumed at a point below the tip and often results in a branched hair. Most commonly described

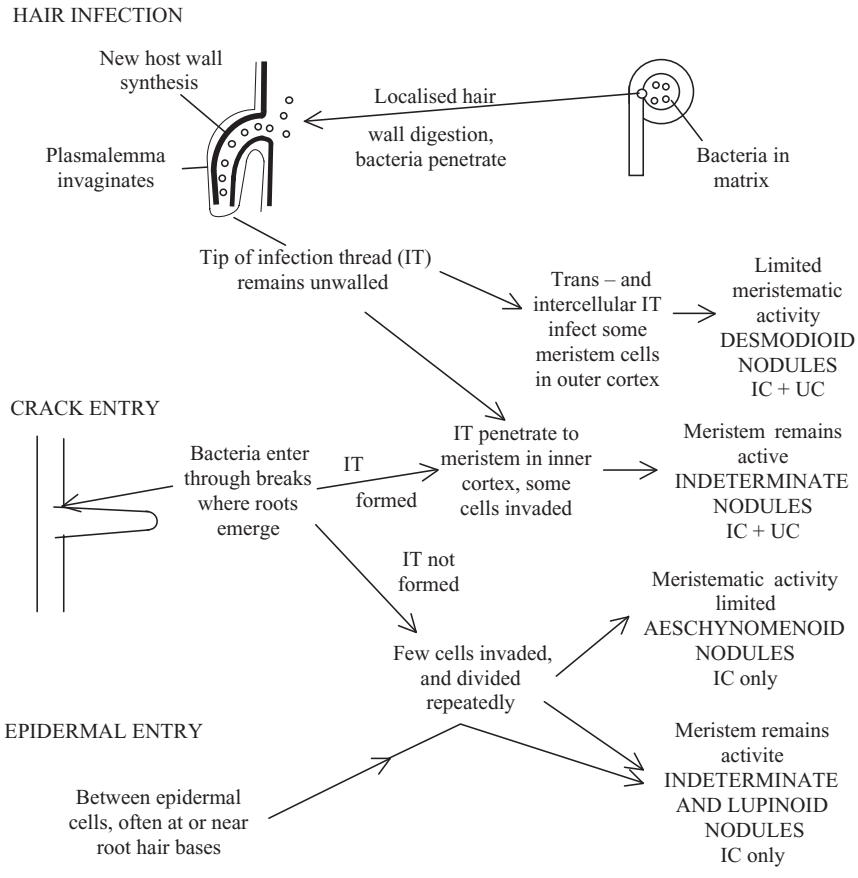

Figure 5.1 Summary of the different pathways leading from rhizobia in soil to formation of different types of nodules. (IC, infected cells; UC, uninfected cells, in infected tissue.) Note that there are two routes from infection to indeterminate nodules, with similar external morphology, but differing internal structure. See also Fig. 3.2.

is the 'shepherd's crook' structure that follows when growth is redirected towards the colony of rhizobia developing below the original apical dome. This process, which can be simulated by local application of Nod factor, is an essential prerequisite for infection thread formation. It is accompanied by the reorganisation of actin filaments in the root hair and root cortex that will become invaded and also by the secretion of glycoproteins (extensins) into the space under the curl. These are cemented by peroxide and thus confine the bacteria to an enclosed space in which they continue to divide (Fig. 5.1). This could build up a pressure that aids penetration against the root hair turgor. The actin filaments form a cytoskeleton (sometimes called the pre-infection thread), which is involved in directing cellulose biosynthesis down the root hair towards the cortex, allowing the bacteria to grow down an emerging infection thread. Between these two events, the original hair wall must be breached and this is likely to

be by localised cellulose digestion. Robledo et al. (2008) showed that *Rhizobium leguminosarum* produced a highly specific cellulase that could breach the root hair wall of *Trifolium repens*, but not of *Medicago sativa* at a localised point beneath the hair tip: thus infection could be coupled to specificity. Specificity at this level could also avoid the induction of host defence responses, elicited by wall-degrading enzymes (Iannetta et al., 1997). Bacteria inside an infection thread are really in an extracellular compartment, surrounded by host cell wall material. Glycoproteins, similar to those in the root hair curl, continue to be secreted into the lumen of the infection thread and to be cemented, probably by H_2O_2 (Jamet et al., 2007) except towards the apex of the thread, where bacteria divide and make their own contribution to the matrix by forming extracellular polysaccharides.

At this stage there are differences between indeterminate and determinate nodules (Table 5.1). In indeterminate papilionoid nodules, cell division is initiated in the inner cortex and some of the cells behind the resulting meristem are infected by branches of the transcellular infection thread. These cells develop into the nitrogen-fixing tissue (see below). In determinate nodules, the meristem develops in the hypodermal region (or middle cortex in the case of *Lotus*) and some cells become invaded by branches of the infection thread and they remain meristematic. Nitrogen fixation commences before the final enlargement of these cells and the initial products are used for nodule growth, unlike those of indeterminate nodules where they are exported (Sprent & Thomas, 1984). Fig. 5.1 outlines these processes. A further difference that is still unexplained is that determinate, ureide-exporting nodules of at least seven genera have crystal cells containing calcium oxalate in their cortices, whereas nodules of five genera with indeterminate nodules do not (Sutherland & Sprent, 1984). Functional differences between these two groups will be discussed later.

5.2 The roles of hormones

In their recent review, Oldroyd & Downie (2008), divide hormonal effects into two types, giving positive and negative regulation. Table 5.2 lists these. Other substances, such as salicylic acid (SA), have also been invoked and suggested to have different effects in indeterminate (pea) and determinate (*Lotus*) nodules (van Spronson et al., 2003). However, Stacey et al. (2006), using a series of plant mutants, showed that SA is involved in the development of both types of nodule, but has pleiotropic effects.

Table 5.2 Hormones involved in nodulation processes. Data from Oldroyd & Downie (2008)

Positive regulators	Negative regulators
Auxins	Abscisic acid
Brassinosteroids	Ethylene
Cytokinins	Jasmonic acid
Gibberellins	

Because of the different locations of developing nodule meristems and hence the progress of infection threads, hormones may have different effects in different types of nodule. For example, ethylene is a negative regulator in indeterminate nodules, because it affects pre-infection thread formation. It also has a negative effect in *Lotus*, where cell divisions occur in the mid-cortex, but has no effect on nodule development in *Phaseolus* beans and soybeans, where divisions occur in the hypodermis (Table 5.1, Fig. 5.1) and no pre-infection threads are formed (Manoury et al., 2008). All the positive regulators are necessary for nodule organogenesis, although exactly how they function is not entirely clear. Possibilities are discussed by Oldroyd and Downie (2008) and include effects on expression of early nodulation (*ENOD*) genes. Local accumulation of cytokinin (the 'secret agent' of symbiosis, Frugier et al., 2008) may stimulate nodule organogenesis at the expense of lateral root development. Supporting this idea, is the conclusion of Mathesius (2008) that high auxin:cytokinin ratios are needed for lateral root development, but low ratios for nodule development. How the negative regulators function is even less clear, except in the case of some of the effects of ethylene (see above). Its effects on *Sesbania* nodulation will be discussed later.

Plant hormones are produced by rhizobia as well as by plant cells and may be involved in nodulation. The possible role of rhizobial cytokinins in crack infection in stem nodulating species of *Aeschynomene* has already been mentioned, but rhizobia are also sources of auxin. Pii et al. (2007) showed that auxin production by *Sinorhizobium meliloti* can increase nodulation in indeterminate (*Medicago sativa*) but not determinate (*Phaseolus vulgaris*) nodules, and that this effect may be mediated by plant-produced nitric oxide (NO), which is also known to be involved in lateral root production in various non-legume plants.

5.3 Autoregulation

Nodules are metabolically very active and a drain on the host plant's resources. Thus it is essential that the plant can control the number of nodules formed. Work on this topic has been aided by the discovery of supernodulating mutants in a number of legumes. Other critical experiments involve use of split-root systems and grafting. Using split-root systems of soybeans for example, it was possible to divide the effects of nitrate into direct effects on nodule formation and indirect effects via the shoot system, which apparently can send signals to the nodulated root, lowering activity of pre-formed nodules (Hinson, 1975, cited by Kinkema et al., 2006). Although most work on the effects of combined nitrogen have been carried out using nitrate, as mentioned elsewhere, in the real world legumes encounter other forms of nitrogen. Ruffel et al. (2008) found that the functional response of *M. truncatula* to nitrogen was different for nitrate and ammonium. It is likely that autoregulation acts in different ways in indeterminate and determinate nodules, because of the different origins of their nodule meristems (Kinkima et al., 2006). Evidence for this comes from grafting experiments between shoots and roots of the two model legumes. These suggested that a shoot-derived factor may be needed for development of nodules in *Medicago truncatula* but not *Lotus japonicus* (Lohar & Vandenbosch, 2005). Roots and shoots certainly speak

to each other all the time and between them control nodulation and other processes. Of the latter, production of nematode galls has been widely studied and many of the cell processes, such as rearrangement of the cytoskeleton and endo-reduplication, seen in nodule formation, are also seen in nematode gall formation (reviewed in Kinkema et al., 2006, but see also Mathesius 2003 and Chapter 3).

5.4 Formation of symbiosomes

Whatever the mode of infection or the passage of bacteria through the nodule cortex, in all cases except some primitive legumes bacteria are 'released' into membrane-bound symbiosomes (Fig. 1.2 B). When infection threads are involved, the tip of the thread develops 'unwalled' droplets and bacteria are surrounded by a plant-derived membrane, equivalent to the plasma membrane (Brewin, 2004), meaning that they remain topologically extracellular. The symbiosome membrane (called the peribacteroid membrane in earlier literature) controls the exchange of material between the two symbionts. Vance (2008) has reviewed the exchange of metabolites between host cells and bacteroids, describing nodules as 'carbon and nitrogen factories' Although the data are mainly derived from model legumes and crop species, there is no reason to suppose that the general metabolism of nodules in other species of legume is fundamentally different, with one possible exception. This concerns the important role of uninfected cells, worked out in most detail for their function in ureide-exporting legumes. How do nodules without such uninfected cells in their infected regions manage? The only definitive evidence for ureide export from nodules comes from the phaseoloid group of legumes (Chapter 1). For these it forms the basis of a possible assay for nitrogen fixation (Unkovich et al., 2008). Reports of ureide export as a measure of nitrogen fixation in other legumes (e.g. Izaguirre-Mayoral & Vivas, 1996) urgently need to be validated, as ureides can be formed in plants in processes not associated with nitrogen fixation. Symbiosomes in host cells are bathed in haemoglobin, which, inter alia acts as an oxygen transport agent, ensuring that the oxygen flux rate to bacteroids is high enough to permit ATP formation, but low enough to avoid inactivation of nitrogenase. In some primitive legumes (Caesalpinioideae and some Papilionoideae; see Chapters 1 and 3), bacteria are not released into symbiosomes, instead remaining in modified infection threads, known as fixation threads. Here they synthesise nitrogenase (E.K. James, personal communication) and fix nitrogen (Sprent et al., 1996).

5.4.1 Bacteroid size and shape

Bacteroid size and shape varies between groups of legumes. In indeterminate nodules of advanced papilionoid legumes, bacteria may undergo considerable endoreduplication of DNA, leading to enlarged size and loss of viability. Such bacteroids occur singly in symbiosomes. On the other hand, in determinate nodules bacteroids are rod shaped, similar in size to their free-living counterparts, retain at least some viability and usually occur in groups of up to eight per symbiosome (Mergaert et al., 2006 and

personal observations). These features are under the control of the host plant. In the vast majority of legumes studied, in all three sub-families, bacteroids are rod-shaped. Pleiomorphy (X, Y and T shapes) seems to be restricted to some, but not all, members of tribes Trifolieae and Fabeae (Vicieae). However, in a survey of bacteroids from many tribes and of all types of nodule morphology, Sprent (2001) found great variation in bacteroid length. Only tribes Phaseoleae, Desmodieae and determinate nodules within Loteae had consistently short rods. There is no information about the DNA content or viability of bacteroids from any of the genera outside the few studied by Mergaert et al. (2006). First reported in *Arachis hypogaea* are large spherical non-viable bacteroids, although recent evidence suggests that these may revert to rod-shaped forms when nodules senesce (Khetmala & Bal, 2005). Similar large coccoid bacteroids, one per symbiosome, have been reported from several, but not all species of *Aeschynomene* (James et al., 2001), but whether or not these are viable is unknown

5.4.2 The role of poly-β-hydroxybutyrate (PHB)

One of the differences between the determinate and indeterminate nodules listed in Table 5.1 concerns the production by bacteria of the reserve polymer, poly-β-hydroxybutyrate (PHB). Trainer and Charles (2006) concluded that PHB is a characteristic of determinate, but not indeterminate nodules. Soybean bacteroids are the classic case, where over 50% of the dry weight of bacteroids can be stored as PHB. It is also often found, but usually to a lesser extent, in nodules of *Phaseolus* beans. However, it is not seen in nodules of several species of the closely related legume genus *Vigna* (Sprent & Gibson, unpublished data). Since PHB is a polymer that is widely produced by bacteria under oxygen-deficient conditions, it could be argued that its accumulation in soybean bacteroids is a sign of inefficiency. This is consistent with the data of Peralta et al. (2004), who found that engineering *Rhizobium etli* so that PHB accumulation was abolished, led to enhanced nitrogen fixation in *Phaseolus vulgaris*. Bacteria in indeterminate nodules can have PHB in infection threads, but not usually in later stages, and it was suggested by Lodwig et al. (2005) that it is used to fuel bacteroid differentiation, and that bacteroids in nodules of plants such as pea use glycogen rather than PHB as a storage product. It is clear that bacteria in indeterminate nodules have the ability to make PHB, and the biochemical pathways for this are set out in Trainer and Charles (2006). Ratcliff et al. (2008) discuss the trade-offs between using reductant to make PHB and to reduce nitrogen and conclude that (at least in *Sinorhizobium meliloti*) PHB is produced to support growth and survival under starvation conditions. In work with *Cyclopia* nodules Elliott et al. (2007b) showed electron micrographs in which PHB was present in nodules formed with a less effective strain of *Burkholderia tuberum*, but not in an effective strain. Gross et al. (2002) studied infection of the mimosoid legume *Anadenanthera peregrina* by rhizobia and found major accumulation of PHB in bacteroids in a symbiosis that was poorly effective. PHB is also often found in nodules of species of *Mimosa* formed with *Burkholderia phymatum* (Elliott et al., 2007a). These references show that PHB accumulation is not confined to determinate nodules, is found in nodules from widely different legumes, can be found in β- as well as α-rhizobia and may be associated with nodules that are not fully effective. Further, there is no

evidence of PHB granules in the determinate nodules of *Lotus* (E.K. James, personal communication).

5.5 Nodules lacking root hair infection

As briefly outlined in Chapter 3, nodule formation without root hair infection is found in tribes Dalbergieae (sensu Lavin et al., 2001), Genisteae and at least some of tribe Crotalarieae, with the formation of either determinate (Dalbergieae) or indeterminate (Genisteae, Crotalarieae) nodules.

5.5.1 Dalbergioid legumes

In Dalbergieae, there are good early studies on *Arachis hypogea* (Chandler, 1978) and *Stylosanthes* spp. (Chandler et al., 1982), which are important grain and forage legumes, respectively. Apart from general observations about the nature of the infected tissue, and the location of nodules in axils of lateral or adventitious roots (Fig. 5.1), all of which are diagnostic characteristics (Sprent, 2000), there are no new data on the details of the infection processes in this group, with the notable exception of the recent work on some stem nodulating *Aeschynomene* species. The presence and function of oleosomes (lipid bodies) in *Arachis* nodules has been of interest in view of the use of the host plant as an oil crop. These studies are summarised in Sprent (1994), with some more recent work in Khetmala and Bal (2005).

Aeschynomene

Aeschynomene is a particularly interesting genus from a nodulation point of view. There are approximately 200 species, distributed almost equally between the Old and New World tropics, with *A. aspera* endemic to Asia and Australia. Recent molecular evidence suggests that there may be two sub-genera (Lavin et al., 2001), although others have suggested three (Klitgaard & Lavin, 2005). All appear to be able to nodulate on roots, but not on stems, using different bacteria (Giraud & Fleischman, 2004; see also Section 4.1.4). A subdivision, based on stem nodulation characteristics was made by Boivin et al. (1997); this classification was extended to other stem-nodulating genera, including *Sesbania*. Three categories were recognised: (1) species where nodulation may occur anywhere on the stem; (2) species where nodulation is largely, but not exclusively on the submerged part of the stem; and (3) species where nodulation is restricted to the lower and submerged part of the stem. Studies have concentrated on species from moist areas, although many are found in areas that are at least seasonally dry (Plate 5.1). In all species, nodulation occurs where adventitious root initials occur, where rhizobia can invade intercellularly. It has not been possible to align the nodule classification of Boivin et al. (1997) with the host species classification of Lavin et al. (2001). However, all nodules are of the aeschynomenoid type, with three variations: (1) in *A. sensitiva* nodules may grow out laterally, forming a collar, as in some species of *Lupinus* and *Lotononis* (Fig. 1.1E); (2) the shape of bacteroids may be coccoid (see above), rod shaped

or possibly both in the same species (Boivin et al., 1997); and (3) in the rhizobia that nodulate them, some of which are photosynthetic (Giraud & Fleischman, 2004). It is possible that coccoid bacteroids are associated with photosynthetic bacteria, but definitive evidence is not available. Infection thread-like structures are occasionally seen, as they may be in other nodules with uniform infected tissue, such as lupin, but they are not involved in the infection process.

5.5.2 Genisteae and Crotalarieae

In members of tribe Genistae that have been studied, infection is via the epidermis, often at the base of root hairs. Species of *Lupinus* have been most widely studied, but nodules of several other genera are similar. Bacteria divide repeatedly as they pass between cells and infect one or a few dividing cells in the root cortex. These infected cells divided repeatedly to form an infected region containing no uninfected cells. Sometimes when several infections occur in the same region, files of uninfected cells remain between segments of infected cells (Plate 2.13). In this group the meristem remains active, either as a single or branched entity, resulting in an indeterminate nodule, similar in external appearance to those on legumes with a hair infection (Fig. 1.1). Evidence from five other genera of Genisteae suggests that these are tribal features (Sprent, 2007). In *Chamaecytisus* (syn. *Cytisus*, Chapter 1), infection threads may be seen in root hairs, but these abort and take no part in the nodulation process (Vega-Hernández et al., 2001). Lupin nodules often have two lateral meristems that grow round and encircle the root, forming the collar nodules that were a favourite experimental tool for some early studies on nodule physiology and biochemistry, because they were easy to remove and harvest in the bulk needed in those days.

In tribe Crotalarieae, evidence is sparse. No records have been found of infection processes, but where nodule structure has been studied, the infected tissue is uniform and infection threads are not seen (Rothschild ,1963, for *Crotalaria juncea* and Yates et al., 2007, for *Lotononis angolensis*). In that there are no known examples of nodules with uniform infected tissue having a root hair infection, it may be inferred that this holds true for at least some of the Crotalarieae.

5.5.3 The special case of Sesbania

Sesbania is genus that is often grouped with *Aeschynomene* because of its apparent ability to form stem nodules (Boivin et al., 1997). However, taxonomically (Chapter 1) and on grounds on nodule structure it is quite distinct. Of the 60 species, half of which are in Africa-Madagascar and the rest distributed in mainly tropical regions around the world, 37 have been recorded as nodulated (Chapter 1). Of these, 5 have been reported as having stem nodules, all from Africa-Madagascar or Asia (Boivin et al., 1997). Of the latter, *S. rostrata* has been extensively studied, but where information is available other species are similar (e.g., James et al., 2001). How are they different from stem nodules on *Aeschynomene* (Plate 5.1), when they are clearly situated on the stem, in rows corresponding to the positions of adventitious root initials (Plate 5.2)? First, when examined in detail they are plumbed into the adventitious root, not the stem; second,

in the formation of their infected tissue, which involves infection threads; and third, in their possession of an apical meristem. The common feature is the infection by rhizobia through cracks where the adventitious roots occur, although there are differences here too. In a detailed study D'Haeze et al. (2003) showed that Nod factors induce the formation of ethylene and reactive oxygen species, leading to localised cell death. These dead cells form an infection pocket, where bacteria proliferate and from which infection threads are formed, infecting cells in the usual way for indeterminate nodules, but with an arrested apical meristem so that superficially the nodules appear aeschynomenoid. Roots, when grown under non-flooded conditions, produce hairs that are infected by rhizobia with the production of normal indeterminate nodules. However, when grown hydroponically, roots produce few hairs and nodulation occurs via cracks where lateral roots are intiated, in exactly the same way as described for nodules formed on stems (Goormachtig et al., 2004). Nodules formed on the stem, but not the root, contain chloroplasts with photosynthetic capacity, but not all of them receive sufficient light to photosynthesise in natural conditions (James et al., 1998). Thus, basically, *Sesbania* nodules are indeterminate, but when grown in moist conditions show arrested development and are superficially aeschynomenoid. Because of their ability to show variations in growth and infection processes, *S. rostrata* nodules have been a very fruitful experimental tool to study nodule developmental processes.

5.6 Other variations in nodule structure

The surface of a nodule is the interface with the root (or sometime the aerial) environment. Some nodules, most notably the desmodioid ones, have a distinct pattern of lenticels through which gaseous exchange occurs (Fig. 1.2A). These lenticels are produced, as in other parts of the plant, by a phellogen (cork cambium). Activity of this phellogen varies in response to environment. For example, in soybeans grown under waterlogged conditions it produces copious aerenchyma and under water stress lenticels collapse (Pankhurst & Sprent, 1975). The phellogens of nodules of many legumes native to dry environments can produce cork. This protects the nodules from desiccation, but also depresses nitrogen fixation (Sprent, 1988). Recovery from this state is only possible for indeterminate nodules, whose meristems resume growth when adequate water supply becomes available (e.g. *Trifolium repens*, Engin & Sprent, 1973). Yet other nodules in woody legumes from various tribes produce one or more tightly packed layers of sclereids in their cortices (Sprent et al., 1989). Such nodules are very brittle and difficult to section, but the function of these sclereids is unclear. It could protect against invasion of pathogens, but one of the many intriguing things about legume nodules is that when developing and when actively fixing nitrogen they appear to be resistant to invasion by pathogens or even mycorrhizal hyphae (Scheublin & Heijden, 2006), although senescent nodules may be colonised.

All legume nodules have their vascular system in the inner cortex, often with a nodule endodermis (that may take the form of a sclereid layer, as in soybeans), but always with an endodermis around each vascular bundle. Individual bundles vary greatly in size and in number of elements within them. Some of the smallest are in phaseoloid nodules, such as in *Vigna*, where the cross-sectional area of an entire bundle can be the

same as that of a cortical cell in the same nodule (Sprent et al., 1989). In nodules of tribes Fabeae and Trifoleae and in *Lupinus* bundles may have vascular transfer cells (Pate et al., 1969). In many woody legumes bundles may be large and much branched (Sprent et al., 1989). Considering the importance of a good transport system to the interchange of nutrient between nodules and their host plants, it is perhaps surprising that, apart from two recent papers on lupin (Łotocka, 2008a, b) gross vascular systems have received little attention for nearly 20 years, most researchers concentrating on what goes on in the infected tissue. However, the interface between the cells of the infected region and the vascular system was investigated by Brown et al. (1995), who quantified symplastic transport in soybean nodules. Walsh (1995) considered apoplastic transport soybean nodules and also discussed the evidence for (and against) interchange of solutes between nodule and the soil solution at the nodule surface. The latter possibility has also been ignored in recent studies, which is also surprising since this is a major interface for nodules. If it is significant (e.g. for nitrate and possibly calcium uptake, Sprent et al., 1987), then it could also be a route by which toxic agents in the soil could affect nodules. E. Gross (personal communication) studied nodules of *Centrosema* in iron mining areas of central Brazil (Plate 5.3) and found their cortices to be impregnated with iron.

5.7 Functioning nodules: the critical role of oxygen

The supply of carbon to the bacteria and the return supply of combined nitrogen to the plant are dealt with in detail in Vance (2008). Clearly for the system to function optimally these have to be closely matched, and how this is done by means of exchange of critical amino acids in the pea nodule has been demonstrated by Lodwig et al. (2003). Overall control of functioning as well as nodule formation and structure is largely under plant control. Possibly the most important way in which this is done is by means of oxygen supply. The role of haemoglobin in fine-tuning the supply of oxygen to the bacteroids was mentioned above, but prior to this there has to be a step down in oxygen concentration from the atmospheric level of 20%, to about 1%. This is achieved by means of both fixed and variable oxygen diffusion resistances. How these operate in various types of nodule has been reviewed by Minchin et al. (2008). These workers also discuss the dilemma of reactive oxygen and antioxidants in nodules. Increasing the resistance to oxygen diffusion by means of the variable resistance means that the host plant can reversibly alter the rate of nitrogen fixation, for example under environmental stresses such as shading, drought, salinity, high and low temperature and phosphate deficiency (Minchin et al., 2008). It has also been invoked as a way in which host plants (soybean in this case) may sanction against any nodules formed by less effective bacteria (Kiers et al., 2008).

5.8 Nitrogen fixation and export of products

Most legumes, whether they are tropical or temperate (or even polar), export amides from nodules to the rest of the host plant. Determinate nodules from the phaseoloid

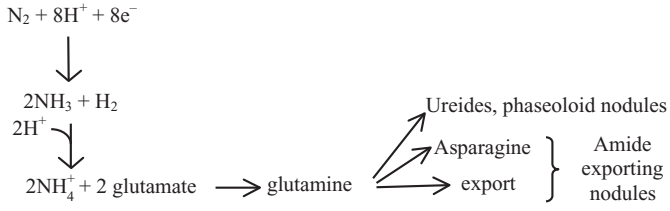

Figure 5.2 Outline of the process of fixation of nitrogen gas into organic nitrogen compounds. For further details see Sprent (2001) or most major textbooks. The initial reduction of nitrogen occurs in bacteroids, with all other reactions taking place in host plant cells. Ureides are allantoin and allantoic acid.

group of tribes, including Psoraleae (Kanu et al., 2008) are unusual in exporting the ureides, allantoin and allantoic acid (Sprent, 2000, 2001). *Lotus* exports amides, which is another reason for its not being a perfect model legume representing determinate nodules. Ureide, but not amide exporters tested also produce β-phenethylamine, especially at flowering stage, but the significance of this compound to the legumes concerned is not clear (Fujihara et al., 2002). The general reactions of nitrogen fixation are summarised in Fig. 5.2.

5.8.1 The hydrogen enigma

It has been known for many years that the production of hydrogen is an inevitable consequence of the nitrogenase reaction (Fig. 5.2). Some bacteroids have the ability to recycle this hydrogen, thus saving some of the energy wasted in its production. This was regarded as a good thing, except that experiments indicated no advantage to nodules having an uptake hydrogenase. A further complication is that the expression of uptake hydrogenase is under control of the host plant (Brito et al., 2008). It has been established that, at least in some circumstances, hydrogen production by legume nodules alters the balance of the soil microflora and may contribute to the benefits of legumes in crop rotation (Dong et al., 2003). This does not always seem to be the case, as Peoples et al. (2008) could find little evidence that hydrogen production by soybeans affected either soybean growth or growth of a subsequent maize crop. In any case, it is difficult to see how hydrogen production is of direct benefit to the legumes producing it, so the jury is still out on this question.

5.9 Nodule effectiveness

Chapter 4 considered some aspects of specificity and competition. Both are relevant to the formation of effective nodules. All are affected by temporal and spatial heterogeneity in the environment. This context-dependent approach to co-evolution is discussed by Heath & Tiffin (2007). Generally, effectiveness is judged by the amount of nitrogen in a symbiotic plant, compared with the same host genotype grown on combined nitrogen. In the best scenario, symbiotic plants may contain as much or even more nitrogen

than when grown on combined nitrogen, and in the worst the nodules fix no nitrogen and are thus parasitic as far as the plant is concerned although the bacteria can obtain considerable benefit. Provorov and Tikhonovich (2003) gave evidence that crop species that have been bred for many years (e.g. peas, soybeans lucerne), often on soils containing combined nitrogen, usually contain less nitrogen when grown symbiotically than when grown on combined nitrogen. On the other hand, 'young' crops such as some vetches (species of *Vicia*) show the reverse. Kiers et al. (2007) looked at the effects of domestication on the effectivess of soybean nodules and found that 'legume defences against poor quality inoculants have apparently worsened under decades of artificial selection' (on fertilised soils).

Measurement of nitrogen in the plant can show ineffectiveness in nodules, even when they appear to be normal in structure, as recently found in the model legume *Medicago truncatula* when grown with *Sinorhizobium meliloti* rather than *S. medicae* (Terpolilli et al., 2008; see also photograph in Sprent & James, 2008). In more extreme cases the number of infected cells in the nodule may be reduced (Gross et al., 2002), and nodules may have less haemoglobin or even no pink coloration at all (Sprent, 2001).There is a close correlation between different forms of haemoglobin and induction of genes necessary for nitrogen fixation (Downie, 2005; Ott et al., 2005). In some cases ineffectivity is accompanied by production of many small nodules; in others nodules are enlarged (Sprent, 2001). In all cases, the bacteria seem able to enter the plant in the normal way, with things going wrong at any stage thereafter. Until the details of normal nodule development are better understood, the exact process that is disrupted when nodules are ineffective will remain obscure. However, ineffectiveness is a very real problem, especially in the tropics (Sprent, 2003) and in large legume genera that can nodulate with a variety of rhizobia (e.g. both African and Australian acacias (Odee et al., 2002, Thrall et al. 2000). Howieson and McInnes (2001), in discussing this problem, also suggest ways in which it may be improved by plant breeding and rhizobial selection. Examples of ineffective nodulation are given in Plate 5.4.

5.10 The bacteria within the nodule – control by the bacteria, plant or both?

The most intensive studies in recent years have been largely conducted on single strains of rhizobia with single host genotypes, as with the model legumes, or in more complex experiments with several such pairs of organisms under varying environments. As far as the plant is concerned, the major requirement is to use carbon resources carefully to give the maximum return in terms of nitrogen fixed. As far as the bacteria are concerned, the need is to maintain reproductive capacity for organisms living in diverse environments. In the last few years, experimental studies on these problems have been supplemented by theoretical considerations. Further, as knowledge of legumes outside the usual run of crop and model species increases, it is apparent that there is great flexibility in the system. Some of the current ideas and dilemmas are considered in this section.

The most extensive sets of papers are from Denison and colleagues in the United States and United Kingdom and Provorov and colleagues in Russia. Kiers et al. (2008) have summarised a number of different hypotheses regarding cooperation between symbionts. These are shared interest, kin selection in the rhizosphere, amino-acid cycling and bacteroid environment, and post-infection sanctions. All are shown to have limitations as a universal answer. Approaching the problem from a slightly different angle, Provorov et al. (2008) suggested that there are two types of gene system operating in the bacteria, partly confounded by horizontal transfer between bacterial genomes. The first system is directed by Darwinian, frequency-dependent selection and operates at the level of host recognition and penetration, i.e, features related to pathogenesis. The second, directed by kin selection, operates at the level of nitrogen fixation and traits beneficial to the host. Another approach has been to consider the relations between the two symbionts as being analogous to collective bargaining between a firm and a worker's union (Akçay & Roughgarden, 2007). Details of these models are beyond the scope of this book. More relevant is the range of levels of effectiveness of nodules in many areas of the globe, for example in different savanna regions (see Section 2.2 in Chapter 2).

5.11 Constraints on nitrogen fixation in agriculture and the environment

Many papers, reviews and even books have been written on factors affecting nitrogen fixation. Most of these have been on crop species, which are usually mesophytes. Thus their growth and nitrogen fixation would be expected to be reduced by all the usual agents: drought, flooding, high and low temperature, salinity and pH extremes. Hartwig (1998) has discussed these in a more ecological context and notes that data for some 'stresses' are ambiguous. Sprent (1999) took up the challenge and reviewed the growth of non-crop species in diverse environments. This section will extend that review and also include some recent work on crop species. There is considerable evidence for the latter, that plants dependent on nitrogen fixation are more sensitive to stress than those grown on combined nitrogen, but this may not be true for legumes that live naturally in an 'extreme' environment.

5.11.1 Waterlogging, drought and salinity

Most crop species such as peas and beans cannot tolerate long periods in waterlogged soil. This is a function of the whole plant, not just nodules. However, as indicated earlier, some legumes occur naturally in wet conditions and some, such as *Discolobium pulchellum* (Lourerio et al., 1994), will only nodulate when submerged. Although it is possible to grow some legumes hydroponically and obtain root hair infection, in natural waterlogged conditions, when oxygen is usually limiting, infection is via wounds associated with lateral root emergence. As discussed above, this may be the primitive, default position.

Both drought and salinity adversely affect root hair development (Sprent & Zahran, 1988). Thus it might be expected that species with a non-hair infection might be more resistant to these stresses. Certainly some, such as *Arachis hypogea*, are quite drought resistant, but another groundnut crop, *Vigna subterranea*, which has a hair infection, is even more drought tolerant (Basu et al., 2007a). Perhaps the most salinity-tolerant legumes are several species of the mimosoid genus *Prosopis* (Felker, 2008), which also has a hair infection (Räsänen et al., 2001). Another saline-tolerant legume, currently being developed for its potential in biodiesel production, is *Millettia pinnata*, being marketed under its synonym *Pongamia pinnata* and known colloquially as pongamia (Scott et al., 2008). This will be considered in more detail under new crops, but is mentioned here because of the possibility that is has a non-hair infection, like its close relative *Lonchocarpus* (Cordeiro et al.,1996). In its native habitat, pongamia has Na^+ and Cl^- contents similar to those of adjacent mangroves (Dagar et al., 1993). Why hair-infected legumes should be drought and salinity tolerant is unclear, but there are two possibilities. First, the studies cited in Sprent and Zahran (1988) are all on crop plants such as *Vicia faba*, from non-stressed environments, so it is possible that the osmotic potential in hairs of tolerant legumes is higher than that of non-tolerant legumes. Second, infection of roots may take place at times when the stress conditions are absent. This is more likely for drought than salinity tolerant species, as even in arid areas, there are periods of rain.

Most rhizobia are tolerant of low levels of salinity – indeed they are adapted to live within the confines of a plant cell whose osmolarity is usually in the range of 300 to 400 $mOsm.kg^{-1}$. However, selection from saline soils can yield strains that will grow in sea water (P.M. Gresshoff, personal communication). Salt tolerance, together with antibiotic resistance, is often used as a preliminary screening tool for rhizobial classification. The problems are more in the plant than the bacterial side of the symbiosis.

5.11.2 Temperature

Both high and low temperatures can be a problem for crop species, especially when agronomists are attempting to extend their range. For many crops, such as soybeans, breeding programmes have produced material suitable for a wide range of temperatures. There are many nodulated legumes that occur naturally in the arctic polar region (Sprent, 2001), and their rhizobia are cold tolerant, sometimes having a higher level of cold shock proteins (Prévost et al., 2004) and/or unusual 'decorations' on their Nod factors (Fig. 4.1; Poinsot et al., 2001). The fact that all legumes from cooler regions appear to depend on nodulation (Section 5.2) is interesting in view of the conclusion of Houlton et al. (2008) that nitrogen fixation globally is constrained by low temperatures. Low temperatures are also found in mountainous regions where plants have, in addition, to cope with low atmospheric pressures. However, in both the Andes and in the Qinghai-Tibetan plateau, where the average altitude is over 4500 m (Hou et al., 2008), legumes seem to grow and fix nitrogen happily when the atmospheric pressure is much less than half that at sea level (Plates 2.12 and 2.13). Considering that nodule functioning is closely related to the partial pressures of the various gases involved, this poses interesting physiological questions.

5.11.3 Edaphic factors

Here much emphasis has been on low pH and the high levels of aluminium, often found in acid soils. A number of legumes occur naturally in such areas, for example species of *Lupinus* in the Mediterranean and many genera and species in some of the Cerrado regions of Brazil (Chapter 2). Both plant and rhizobial genotypes have been selected from wild material and, again especially in the case of lupins, have produced many commercial cultivars. There are other legumes such as white clover (*Trifolium repens*) which are very intolerant of aluminium. Thus, as Australian agronomists have been doing for many years, collecting plant material from areas that naturally have the adverse conditions is the best procedure (see also Chapter 2). High pH is also a problem in many soils, often coupled with high levels of various minerals, but again, there are legumes adapted to such conditions (Plate 2.4).

Hundreds of papers have been written on the need of nodulated legumes for high levels of available soil phosphorus. Without disputing any of these, it must be emphasised that there are numerous nodulated legumes that are native to soils with very low available phosphorus and for some, 'normal' soil levels of phosphorus are toxic (Sprent, 1999). The latter include *Stylosanthes humilis*, where 1000 μM of phosphorus inhibited nodulation, which was normal at 62.5 μM (Date & Ratcliffe, 1989). Recent work suggests that the toxicity may be because such species are unable to down-regulate their high-efficiency phosphate uptake systems (Lambers et al., 2007). Nevertheless, when introducing crops such as soybeans into new areas (particularly in the tropics), additional phosphorus may be one of the keys to success. The whole topic of nitrogen fixation in tropical cropping systems has been well covered by Giller (2001) and will not be covered in detail here. It remains one of the iniquities of the world that the poorest countries are the most in need of nitrogen-fixing crops and yet comparatively little research is being conducted on most of the crops that are adapted to their local conditions. However, the tide is beginning to turn and a later section will consider some of the crops that have potential for such areas. Apart from the obvious humanitarian needs, with the onset of global climate change a better understanding of how legumes function in adverse conditions is a sensible strategy for general food security.

5.12 Legumes, pests and pathogens

Legumes do not grow alone and their interactions with other species – plant, animal and microbial – need further study. Because of their high nitrogen content, legumes are a prime target for many pests and pathogens, many of which, such as beetles attacking stored grain legumes, have been extensively studied. The production of toxins by legumes to discourage herbivory has also been well studied, for example the production of fluoroacetate by some Australian legumes (see Section 1.3.5 in Chapter 1). However, the situation may be complex. In the case of *Oxytropis sericea* (white locoweed), the toxic alkaloid swainsonine is synthesised inside the legume by a fungal endophyte *Embellisia* sp. Its production is enhanced by the presence of effective nodulation by rhizobia (Valdez Barillas et al., 2007). Some weevil larvae specifically attack the pink centre of

nodules, which could be their equivalent of a good steak. Bean leaf beetles, a pest of soybeans, can also attack other parts of the plant, including nodules (Lundgren & Riedell, 2008). Angiosperm parasites such as *Orobanche crenata* can decimate entire crops of grain legumes. Paradoxically, legume roots may secrete a class of substances known as strigolactones, which can stimulate the germination of plant parasites, but these substances are also important for the recognition between the legume and AM fungi (Yoneyama et al., 2008). On the other hand, it has recently been found that some strains of *R. leguminosarum* in association with pea plants produce phenolic compounds that decrease the germination of parasite seeds (Mabrouk et al., 2007). Nematodes,are best known as pests of plants and animals, but many of them live saprophytically in soil and contribute to nutrient cycling. Some of these are attracted to legume roots in response to volatiles produced by the roots and carry with them rhizobia capable of nodulating these roots (Horiuchi et al., 2005). Rhizobia also produce plant growth-promoting substances, and these may enhance the ability of host plants to grow in soils contaminated with heavy metals such as arsenic (Reichman, 2007).

Chapter 6

Some Legumes for the Future?

There have been repeated attempts to sponsor new legume crops, especially for resource-poor peoples in tropical countries. In 1979, the National Academy of Sciences (USA) produced a seminal work describing many legumes with potential for food and forage use in the tropics (Anon, 1979). Slightly more recently they produced two volumes devoted to firewood crops, acknowledging the importance of these as a source of energy, often for cooking (Anon, 1980, 1983).

Native peoples in all continents have made good use of their indigenous legumes for millennia. A search of the literature has shown that very few of the crops listed in Anon (1979) have been developed, although things are at last beginning to change. Instead, presumably because of the economic benefits to seed producers, major crop species such as soybeans and peanuts (groundnuts) have been introduced worldwide. With impending world food shortages and climate change, this is not a healthy situation and programmes to develop some of these underutilised resources are urgently needed. With Africa in mind, the National Academy of Sciences has produced three new volumes 'Lost Crops of Africa', the second volume of which is devoted to vegetables (Anon, 2006). Table 6.1 lists many of the tropical legumes with potential used for human food, most of which are covered in Anon (2006) for Africa or in Anon (1979), where the coverage is global. Since the earlier publications, some of the species names have been changed. Where this is the case, both names are given. Where there has been some recent work done, or where the plant has particularly useful characteristics, they will be discussed further; otherwise readers are referred to the volumes produced by the National Academy. All the species listed are from tribe Phaseoleae. Most of the plants listed have many local names, but only the most widely used ones will be given here. Table 6.2 lists legumes of other species that are considered to have potential, but that do not nodulate, so will not be considered further.

In this chapter, some of the uses of nodulated legumes for human food, forage, and other purposes such as pharmaceuticals will be outlined. The emphasis is on the tropics and sub-tropics, where the needs are most acute and where there is an abundance of underutilised species. Agroforestry will not be covered, nor will the use of legume fallows, as they are extensively covered in the literature (e.g. Giller, 2001). Use of legumes for timber has also been well covered in the various publications of the Nitrogen Fixing

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Table 6.1 Legume species with potential for human food in tropical areas. Where the species epithet has been changed, it is noted as 'syn' – for most species there are many local common names. Only the major use is given; + indicates that there are several other uses. All are from tribe Phaseoleae

Genus	Species	Common name	Main edible part
Apios	*americana*	Potato bean	Tuber
Cajanus	*cajan*	Pigeon pea	Pods, seed+
Canavalia	*ensiformis*	Jack bean	Seed
	gladiata	Sword bean	Seed
Flemingia	*procumbens* syn *vestita*	None found	Tuber
Lablab	*purpureus*	Hyacinth bean	Seed+
Macrotyloma	*geocarpum*	Kersting's groundnut	Seed
Pachyrhizus	*erosus*	American yam bean	Tuber, seed
Phaseolus	*acutifolius*	Tepary bean	Seed
	dumosus	Year bean	Seed
	lunatus	Lima bean, butter bean	Seed
	vulgaris	Common bean	Pods and seed
Psophocarpus	*tetragonolobus*	Asparagus pea Winged bean	All parts
Pueraria	*phaseoloides*	Kudzu	Tuber
Sphenostylis	*stenocarpa*	African yam bean	Tuber, seed
Vatovaea	*pseudolablab*	None found	Tuber
Vigna	*aconitifolia*	Moth bean	Seed
	angularis	Adzuki bean	Seed
	heterophylla syn *ambacensis*	None found	Tuber
	lanceolata	None found	Tuber
	luteola syn *fischeri*	None found	Tuber
	marina	Coast bean	Tuber
	mungo	Black gram	Seed
	radiata	Mung bean, green gram	Seed
	umbellata	Rice bean	Seed
	subterranea	Bambara groundnut	Seed+
	unguiculata	Cowpea	Seed+
	ssp. *sesquipedalis*	Long bean	Pods, seed+
	vexillata syn *lobatifolia*	None found	Tuber

Table 6.2 Some legumes that have been proposed for development, but which do not nodulate

Common name	Scientific name	Comment
Carob	*Ceratonia siliqua*	Drought resistant, multiple uses
Locust bean	*Parkia biglobosa*	Edible fruit
Marama bean	*Tylosema esculentum*	Drought tolerant, nutritious tubers
Tamarind	*Tamarindus indicus*	Multiple use, especially fruit pulp
Ye-eb	*Cordeauxia edulis*	Drought tolerant, edible 'nuts'

Tree Association (which no longer publishes), but it should be noted that there are some mistakes in their publications concerning legumes that are assumed to fix nitrogen, but do not. More recently CSIRO, Australia, published NFTNews on behalf of the International Union of Forest Research organisations (IUFRO), but the editor (A. Kalinganina) is now operating from Mali. Copies are now only being produced electronically and can be obtained (free of charge) from http://www.iufro.org/science/divisions/division-2/20000/20800/20802/newsletters/. However, there is relatively little information in any of these publications on selection for improved nitrogen fixation (Sprent, 2005). For example, *Dalbergia sissoo* is widely grown in India and many publications on its management have been published, but only recently is serious attention being given to positive use of its nodulating ability (e.g. Devagiri et al., 2007). There is now an interest in income-generating products from legume trees other than timber. An example is the widely used food additive, gum Arabic, from *Acacia senegal*, for which there is an active EU programme (http://inco-acaciagum.cirad.fr) to find improved germplasm and growing conditions to achieve higher and more reliable production (D.W. Odee, personal communication).

6.1 Human food

Developed countries tend to use only one part of a legume, usually the pod or seed for food, and reject the rest. In the developing world almost the whole plant (leaves, flowers, fruits, tubers) may be eaten by humans with anything remaining being fed to animals or used as fuel.

6.1.1 Vigna *spp.*

Vigna subterranea, commonly known as bambara groundnut, is an African native, with underground pods (Plate 6.1), very popular as a food source. However, until recently it was being displaced by peanut/groundnut. In their excellent account of bambara groundnut, Anon (2006) suggest two possible reasons for its neglect. The first is that it may be regarded as a poor person's crop, but the second, more likely one is that 'it seems largely due to the lack of familiarity by those setting the research agenda – especially outside Africa'. A cynic might also add that there are vested interests in using peanuts. Bambara groundnut is more drought tolerant than peanut, and can tolerate more infertile soils. Although having quite a lot less oil and a little less protein, it is nutritionally very balanced and can form the sole source of food for humans. The main problem is that current yields are low, because there has been very little effort to improve them. Some attempt to redress this is being made under an EU INCO-DEV programme 'BAMLINK', involving workers in both Africa and India. This research is using both traditional and modern molecular methods (Basu et al., 2007a, b), and it is suggested that eventually a fourfold increase in yield may be possible (S. Mayes, personal communication).

One legume that was widely promoted about a decade ago was *Vigna unguiculata* ssp. *sesquipedalis*, the long or winged bean. Its advantages are that all parts are edible,

including flowers. Its disadvantages are that it is not tolerant to waterlogging and yet it needs a high rainfall. It is now cultivated worldwide and is a fashionable crop in the United States and elsewhere, but it is fair to say that it has not been the miracle plant for Africa for which it was hailed. More realistically cowpea, *V. unguiculata*, is a crop that grows well in Africa, even in low rainfall areas, where it is often grown together with maize (Plate 6.2). It is estimated that 200 million people in sub-saharan Africa eat cowpeas when they are available (Anon, 2006). It has already been the subject of considerable agronomic research and is being grown in South America and parts of Asia, where it is usually known as black-eyed pea. Yields are still low and there are major problems with insects, but the potential is great.

In the Indian sub-continent, other species of *Vigna* are in widespread use, including green and black gram. However, perhaps the most interesting plants with potential are those that produce both edible seed and tubers. Two of these are the African and American yam beans (Table 6.1).Tubers are generally are both good to eat and a way for the plant to survive adverse conditions such as drought, because they can produce new shoots after rain. Plate 6.3 shows tubers of *Vigna vexillata*, which was widely used as 'bush tucker' by Australian Aborigines and which is currently being assessed for development (Grant et al., 2003). Most of the legumes listed in Table 5.3, but especially species of *Vigna*, appear to nodulate freely (Plate 6.4). Normally nodulated by bradyrhizobia, recent studies have found salt-tolerant strains of fast-growing rhizobia from coastal sand dunes in India that perform well on cowpea and other legumes (Arun & Sridhar, 2004).

6.1.2 Other phaseoloid legumes

There is certainly a move to capitalize on the wider use of legumes, especially when they can be grown on marginal land. An example is the work of Sridhar & Bhagya (2007) using *Canavalia maritima* growing on coastal sand dune vegetation in India. This plant not only stabilises soil, it has edible pods, can be used for forage, as a green manure and has bioactive compounds for potential medicinal use. As it is pan-tropical, growing also in parts of Africa and Northern Australia, it is a good candidate for further development.

Apios americana has an interesting history. Its tubers were a staple food of native Americans and it helped the early European settlers survive their first few winters in North America. Following the Irish potato famine in 1845, it was introduced into Europe and grew well. Now it has largely fallen out of fashion, but its potential, and that of related species was raised recently by Vietmeyer (2008).

Pigeon pea, *Cajanus cajan*, has a long history of cultivation, but still needs developing to achieve its full potential. It is one of the crops highlighted in Anon (2006). It is a multi-purpose species that nodulates freely, a short-lived perennial though often grown as an annual. It has a deep root system, can access poorly available soil phosphorus (Sprent, 1999), yields nutritious seed, can be browsed by animals and produces firewood. The Internationational Institute of Tropical Agriculture (IITA) is developing markers for the African yam bean (*Sphenostylis stenocarpa*), with a view to producing better cultivars (Moyib et al., 2008). The tubers of this plant 'look like sweet potatoes, but taste more

like Irish potatoes'. Plate 6.5 shows tubers of *Pueraria tuberosa*, together with nodulated roots. These tubers may grow to 35 kg and have a high protein content (Anon, 1979), but in parts of India are mainly used as a source of drugs against malaria and as contraceptives (H.S. Gehlot, personal communication).

Erythrina is a genus usually known for its fine tree species, which have multiple uses. In a monograph edited by Westley and Powell (1993), many of these are listed, but no mention is made of the one species known to have edible (most are poisonous) seeds, *E. edulis* (Plate 6.6). These seeds have been used since the time of the Incas in Peru, Venezuela and neighbouring areas. They can be harvested at a time when no other such foods are available and thus fill an essential gap. As well as providing food, the small trees are also used for construction, poles for fencing, animal fodder, mulching and as shade for other crops. Its potential for developing regions is outlined in 'Lost Crops of the Incas' (Anon, 1989). Other crops described in this publication include a type of *Phaseolus vulgaris*, known as the 'popping bean' because the seed is roasted rather than boiled at altitude when the air pressure is too low to cook them in a reasonable time and without using too much fuel. When roasted they 'pop' rather like popcorn.

6.2 Forage legumes

In temperate regions forage legumes have been developed for many years. Current work is looking at developing new species for use in tropical and warm temperate areas, especially those with low rainfall. Of these, some of the more interesting are those adapted to acidic infertile soils, such as found in parts of South Africa and southwest Western Australia (see also Chapter 2). Howieson et al. (2008) discuss the rationale for developing these species, some of which nodulate with non-classic rhizobia (see Section 4.2). At the Centre for Rhizobium Studies (CRS) in Murdoch University, Perth Western Australia, a range of perennial forage legumes is being developed for use in animal production. The ideal plant for this must be able to grow well in annual rainfall of 150 to 250 mm, be highly fecund, with easily harvested seed, acid as well as drought tolerant, palatable to livestock and, perhaps most important, to nodulate effectively with acid-tolerant rhizobia. One of several species that is showing great promise is *Lebeckia ambigua*, which has an extensive woody root system (evolved for regeneration after fire) that generates succulent shoots, palatable to livestock (Plate 6.7). Although producing plenty of seed, it is thought to be a low risk for weediness (Section 2.6) (J.G. Howieson, personal communication). It nodulates freely with an as-yet-unnamed species of *Burkholderia*. Other South African species of genera *Lotononis* (Yates et al., 2007) and *Lessertia* (Howieson et al., 2008) also have potential for acidic soils. Further details of this and other related work can be found on the CRS website. An Australian native species, *Cullen australasicum*, also shows potential as a low rainfall perennial pasture species. In this case its low palatability to sheep was considered an advantage, to prevent over-grazing (Dear et al., 2007).

In order to develop new legumes for agriculture, Howieson et al. (2008) identify five key steps. First, why they are needed and why current species are failing; second, what are the relevant social and economic issues that may affect its adoption; third,

identification of germplasm on which to experiment; fourth, selection or breeding of both legumes and rhizobia that are adapted to each other and to the target soil and climatic conditions; and fifth, assessing the implications of introducing new plant and rhizobial material, including the threat in invasiveness. All of these steps involve relatively old-fashioned agronomy, but can be greatly assisted by modern techniques, in particular for screening germplasm.

6.3 Pharmaceutical uses

Legumes have been used to treat various ailments, for contraception and many other purposes, including poisons, for thousands of years. For example, insecticides such as derris are made from legumes. Many of these uses are described in Allen and Allen (1981). However, there is now renewed interest in the potential therapeutic value of plants generally, including legumes. The markets can be huge, in both conventional and alternative medicine. Many of the species targeted are from developing countries, where it is important that the indigenous knowledge is appropriately rewarded. It is also essential that proper trials are conducted as to the efficacy of the alleged drug. Of the many plant extracts currently being evaluated, one that appears to hold some promise is from *Sutherlandia frutescens*, sometimes called *Lessertia frutescens* and commonly known as 'cancer bush' (Plate 6.8). This has been used for many years as a folk medicine by people in South Africa, but now there is sufficiently strong evidence to suggest that clinical trials be conducted to assess its potential for the control of various diseases, including some forms of cancer (van Wyk & Albrecht, 2007). Howieson et al. (2008) lists a number of other legumes that appear to give health benefits, including extracts from the rootstock of *Eriosema kraussianum* that are said to have 75% of the effect of Viagra (on rats).

6.4 Other uses

There is an increasing interest in teas, other than from *Camellia sinensis*, especially those that have possible health benefits, such as being caffeine free. Two of the latter are from nodulated legumes indigenous to South Africa. Best known is rooibos, or red bush tea, made from the shoots of *Aspalathus linearis*. This plant can grow on some highly infertile soils, producing cluster roots, nodules and mycorrhizas to aid its nutrient acquisition. Although originally harvested from wild material, selected germplasm is now widely grown (Plate 2.11), processed on an industrial scale (Plate 6.9) and exported throughout the world, being common on supermarket shelves. There are environmental concerns in some areas that the native flora is being displaced and that too much biomass is being harvested, leading to death of the *A. linearis* plants (personal observations). Less well known is honeybush tea, for which the major species used commercially are *Cyclopia intermedia* and to a lesser extent *C. subternata*, although a number of others are used for home consumption. Much of the crop is still harvested from wild material, but field-scale production is now getting underway and production is rising rapidly, both

for the home and export markets. Perhaps inevitably for plants such as these legume teas, which can grow naturally on very poor soils, there is a niche market for organic production. Since this market tends to be relatively small volume, it is well suited to community-based production and can be important for sustaining local developments (Nel et al., 2007).

There are serious concerns about farming carnivorous fish such as salmon on feed that consists largely of wild fish such as anchoveta, because of its unsustainablility. Various grain legumes, including soybeans, peas and lupins are being considered in Europe and elsewhere, with lupins generally being preferred. The Australian Government has a programme looking at lupins for all types of aquaculture, both fin fish and shellfish, details of which can be found on http://www.fish.wa.gov.au/docs/op/op031/fop/031.pdf. Different fish species may vary in the acceptability of different grain legumes (Glencross et al., 2004). In warmer waters, herbivorous freshwater fish such as Tilapia can be farmed and these can use legumes such as prunings of *Calliandra* from agroforestry as a part of their diet (J. Wilson, personal communication).

Natural dyes have been in use for millenia, but renewed interested in them for providing local income is being shown. In Madagascar, Natal indigo, made from the leafy shoots of *Indigofera arracta*, is being developed and is proving to be a high-quality product, with good colour fastness in light, unusual for a blue dye (Borus, 2008).

Production of bioethanol and biodiesel for use in road and other forms of transport is currently very newsworthy, largely because of diverting agricultural land away from growing food crops. However, *Millettia pinnata* (pongamia) is a small tree from India that grows profusely on land, including mangrove swamps, that is unsuitable for crops. It fruits profusely and its seeds have a high content of oil that needs very little processing to produce an excellent type of diesel. It nodulates well with bacteria that can grow in pure seawater and is currently under extensive evaluation in Australia and elswhere (Scott et al., 2008; P.M. Gresshoff, personal communication).

As well as using legumes as a source of various products, those adapted for harsh environments could provide genetic material to be introduced into other crops, either by conventional breeding or by genetic engineering. For example, one of the uses suggested for *Canavalia maritima* (see Section 6.1.2) was as a source of genetic material to confer salt resistance (Sridhar & Bhaghy, 2007). Many people in developing countries cannot understand why Europe is so averse to using genetically modified plants. Neither can I.

Finally, on a global scale, legumes can have a major role to play in providing ecosystems services, particularly in maintaining a sufficient supply of reduced nitrogen under increasing atmospheric carbon dioxide (Jackson et al., 2008). As Sisti et al. (2004) point out, if soil is to be used as a carbon store, there may be an important role for managing legumes to optimise carbon sequestration.

Appendices

Introduction and cautionary notes

These appendices have been added as a guide to the current state of play on nodulation. Readers should also check the GRIN (Germplasm Resources Information Network) database at http://www.ars-grin.gov/~sbmljw/cgi-bin/taxnodul.pl.

The GRIN database is a vast compilation from records in the literature and the authors have had access to much of the 'grey' literature that is not readily available to the general reader. However, particularly when looking at a genus for which there may be doubt as to its nodulation status, readers should go back to the original reference (which can be found in the GRIN database) and check the evidence given, especially for all Caesalpinioideae and the more basal groups of the other sub-families. There are many false reports of nodulation based on unexamined outgrowths on roots (illustrated in Sprent, 2001). Where possible, I have checked my lists against those in GRIN, almost exclusively only at the species level, and amended them as appropriate, with the notable exception of *Acacia* s.l. In the case of *Leucaena*, nearly half the records have been taken from GRIN. This is because their reports were in a list of potential inoculants for *Leucaena* spp., not readily available to me. On the other hand, most of the reports for *Mimosa* come from recent studies from our international programme on this genus. I am grateful to colleagues, especially those in S. Africa and W. Australia for permission to use their unpublished records. Numerous variations remain between data in GRIN and those given here, because of uncertainties in legume classification (e.g. GRIN accepts *Balizia*, but following Lewis et al. (2005) it is included here in *Albizia*) and access to different sources of information. My lists include many new records that I hope will join GRIN shortly. Where there are negative reports for a species from a genus otherwise uniformly nodulated, it might mean that conditions were not right for nodulation when the record was made. Reports from much of the older literature are subject to possible plant mis-identification. It was not standard at that time (as it should be now) to lodge specimens at a suitable herbarium, so that future studies can check the identification.

The GRIN database is excellent for checking synonyms and is kept reasonably up-to-date on this. However, plant taxonomists have a tendency, especially with new molecular methods, to change the assignment of specimens to genera and species. This in the long run is a good thing, but is not always helpful to the less specialised reader. Another potential pitfall is the authority quoted for the species. Check this carefully, because the same species name may carry different authorities and end up as different species or even genera. Examples of within-genera variations in GRIN can be found under *Desmodium* and between genera for *Lonchocarpus*.

For most reports subsequent to my 2001 book I have added references. Readers are invited to contact me on jisprent@btinternet.com for further details or queries.

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Appendix I: Caesalpinioideae

Campsiandra

C. comosa Benth. and var *laurifolia* (Benth.) Cowan

Chamaecrista

C. absus (L.) Irwin & Barneby
C. adiantifolia (Benth.) Irwin & Barneby
C. biensis (Stey.) Lock
C. calycioides (Colladon) Greene
C. ciliolata (Benth.) Irwin & Barneby
C. conferta (Benth.) Irwin & Barneby var. *virgata* (Irwin & Barneby)
C. coradinii Barneby
C. cultrifolia (Kunth) Britton & Rose
C. cytisoides (Colladon) Irwin & Barneby var. *blanchetii* Irwin & Barneby
C. decumbens (Benth.) Irwin & Barneby
C. dentata (Vog.) H.S. Irwin & Barneby
C. desvauxii (Colladon) Killip var. *brevipes* (Benth.) Irwin & Barneby
C. desvauxii var. *circumdata* Irwin & Barneby
C. desvauxii var. *desvauxii* (Colladon) Killip
C. desvauxii var. *latistipula* (Benth.) G.P. Lewis
C. desvauxii var. *linearis* (Irwin) Irwin & Barneby
C. desvauxii var. *mollissima* Irwin & Barneby
C. dentata (Vogel) Irwin & Barneby
C. diphylla (L.) Greene
C. duartei (Irwin) Irwin & Barneby
C. ensiformis (Vell. Conc.) Irwin & Barneby
C. fagonoides var. *macrocalyx* (Irwin & Barneby)
C. falcinella (Oliv.) Lock
C. fasciculata (Michx.) Greene
C. fenarolia (Mendonca & Torre) Lock
C. flexuosa (L.) Greene
C. geminata (Benth.) Irwin & Barneby
C. gracilior (Ghesq.) Lock
C. hispidula (Vahl.) Irwin & Barneby
C. hirsuta Tlusty et al. (2004)
C. isidorea (Benth.) Irwin & Barneby
C. kunthiana (Schldl. & Cham.) Irwin & Barneby
C. leptadenia Cockerell
C. leschenaultiana (DC.) Degener
C. mimosoides (L.) E. Greene
C. neesiana (Benth.) Irwin & Barneby var. *subnitida* (Taub.) Irwin & Barneby
C. negrensis (Irwin) Irwin & Barneby
C. nictitans (L.) Moench subsp. *disadena* (Steud. Irwin & Barneby
C. nictitans subsp. *nictitans* (L.) Moench
C. nomame (Sieb.) H. Ohashi
C. orbiculata (Benth.) Irwin & Barneby
C. orbiculata var. *orbiculata* (Benth.) H. Irwin & Barneby
C. parva (Stey.) Lock
C. patellaria Greene
C. polytricha (Brenan) Lock
C. pumila (Lam.) K. Larsen
C. quarrei (Ghesq.) Stey. = *C. stricta* E. Mey.
C. ramosa (Vogel) Irwin & Barneby
C. ramosa var. *curvifolia* (Vogel) G.P. Lewis
C. repens (Vogel) Irwin & Barneby
C. rotundifolia (Pers.) Greene
C. rotundifolia (Pers.) Greene var. *rotundifolia* (Pers.) Greene
C. serpens (L.) Greene
C. serpens var. *serpens* (L.) Greene
C. stenocarpa (Vogel) Standl.
C. swartzii (Wikstrom) Britton
C. viscosa (Kunth.) Irwin & Barneby var. *major* (Benth) Irwin & Barneby
C. wittei (Ghesq.) Lock

Chidlowia

C. sanguinea Hoyle Diabate et al. (2005)

Dimorphandra

D. conjugata (Splitg.) Sandwith K.
D. cordata Ducke
D. campinarum Ducke Faria pers comm to J.H. Kirkbride (2006)
D. davisii Sprague & Sandwith
D. exaltata Schott
D. jorgei M.F. Silva
D. macrostachya Benth.
D. mollis Benth.
D, parviflora Benth.
D. vernicosa Benth.
D. wilsonii Rizzini M.R. Scott-Mutti pers. comm. (2006)

Erythrophleum

E. africanum (Benth.) Harms
E. ivorense
E. suavolens (Guill. & Perr.) Brenan

Melanoxylon

M. brauna Schott

Moldenhawera

M. floribunda Schrader

Sclerolobium

now included in *Tachigali*

S. albiflorum Benoist
S. aureum var. g*randiflorum* Dwyer
S. chrysophyllum Poeppig
S. densiflorum Benth.
S. hypoleucum Benth.
S. melinonii Harms
S. micropetalum Ducke
S. paniculatum Vogel
S. paraense Huber
S. rugosum Benth.

Tachigali

T. cavipes (Benth.) Macbr. as *T. paniculata* var, *panculata* Aubl.
T. macrostachya Huber Faria, pers. comm. to J.H. Kirkbride (2006)
T. paniculata var *alba* (Ducke) Dwyer

Appendix II: Mimosoideae

Abarema

A. adinophora (Ducke) Barneby & J.W. Grimes
A. auriculata (Benth.) Barneby & Grimes
A. barbouriana (Standl.) Barneby & Grimes var. *arenaria* (Ducke) Barneby & Grimes
A. bigemina (L.) Kosterm. = *Archidendron bigeminatum*
A. brachystachya (DC.) Barneby & Grimes,
A. campestris (Benth.) Barneby & J.W. Grimes S.M. de Faria, pers. comm. to J.H. Kirkbride (2006)
A. cochleata (Willd.) Barneby & Grimes, formerly *Inga cochleata* Willd.
A. cochliacarpos (Gomes) Barneby & Grimes
A. filamentosa (Benth.) Pittier
A. floribunda Barneby & J.W. Grimes S.M. de Faria, pers. comm. to J.H. Kirkbride (2006)
A. jupunba (Willd.) Britton & Killip Moreira et al. (1992) It is not clear to which var. this report refers. Allen & Allen (1981) list *Pithecellobium trapezifolium* Benth. as nodulated: this species has now been reclassified as *A. jujunba* var. *trapezifolia* (Vahl) Barneby & Grimes.
A. macradenia (Pittier) Barneby & J.W. Grimes. Barrett & Parker (2005)
A. mataybifolia (Sandwith) Barneby & Grimes
A. turbinata (Benth.) Barneby & Grimes

Acacia sensu lato

Nodulated members of sub-genus Acacia
A. abyssinica Benth. and subsp. *calophylla* Brenan
A. amythethophylla A. Rich. = *A. macrothyrsa*
A. anceps DC.
A. arabica Willd. = *A. nilotica* subsp. *indica*
A. aroma Hook. & Arn.
A. borleae Burtt Davy
A. caven (Molina) Molina
A. cochliacantha Willd.
A. constricta Benth.
A. cornigera (L.) Willd.
A. davyi N.E.Br.
A. ehrenbergiana Hayne
A. exuvialis Verd.
A. farnesiana (L.) Wild.
A. flexuosa Humb. & Bonpl. = *Prosopis flexuosa* DC.
A. gerrardii Benth.
A. grandicornuta Gerstner
A. gummifera Willd.
A. hebeclada DC. and subsp. *hebeclada* DC.
A. hockii De Wild. as *A. orfota* (spelled *orfoto* in Allen & Allen, 1981)
A. horrida (L.) Willd.
A. karroo Willd
A. jacquemontii Benth. H.S. Gehlot, pers. comm. (2007)
A. kirkii Oliv. and subsp. *kirkii* Oliv.
A. leucophloea (Roxb.) Willd.
A. luederitzii Engl., vars. *luederitzii* Engl. and *retinens* (Sim) J. Ross & Brenan
A. macracantha Willd.
A. macrothyrsa Harms = *A. amythethophylla*
A. nubica Benth. = *A. oerfota*
A. nebrownii Burtt Davy
A. nilotica (L.) Del. and subspp. *kraussiana* (Benth.) Brenan and *indica* (Benth.) Brenan
A. orfota Schweinf. = *A. hockii*
A. permixta Burtt Davy
A. prasinata A. Hunde

A reficiens Wawra and subsp. *reficiens* Wawra
A. rehmanniana Schinz
A. robusta Burchell and subspp. *clavigera* (E. Mey.) Brenan and *robusta* Burchell
A. schottii Torr.
A. seyal Del.
A. sieberiana DC. and vars. *vermoensenii* (De Wild.) Troupin and *woodii* (Burtt Davy) Keay & Brenan
A. stuhlmannii Taub.
A. swazica Burtt Davy
A. tenuispina Verd.
A. tomentosa Willd.
A. tortilis (Forssk.) Hayne and subspp. *heteracantha* (Burchell) Brenan, *raddiana* (Savi) Brenan and *spirocarpa* (A. Rich.) Brenan
A. xanthophloea Benth.

Nodulated members of sub-genus Aculeiferum

A. angustissima (Mill.) Kuntze = *Acaciella angustissima* (Mill.) Britton & Rose. Rico & Bachman, (2006)
A. bahiensis Benth.
A. catechu (L.f.) Willd.
A. caffra (Thunb.) Willd.
A. caesia (L.) Willd.) as *A. intsia*
A. chariessa Milne-Redh.
A. dolicostachya S.F. Blake
A. galpinii Burtt Davy
A. goetzei Harms subspp. *goetzei* Harms and *microphylla* Brenan
A. hereroensis Engl.
A. kraussiana Benth.
A. martii Benth.
A. mellei Verd. = *A. hereroensis*
A. mellifera (Vahl) Benth. and subsp. *detinens* (Burchell) Brenan
A. modesta Wall Athar (2005) *A. multipinnata* Ducke
A. nigrescens Oliv.
A. pennata (L.) Willd.
A. polyacantha Willd. and subsp. *campylacantha* (Hochst. ex A. Rich,) Brenan
A. polyphylla DC
A. praecox Griselb.
A. rovumae Oliv.
A. senegal (L.) Willd. and vars. *leiorhachis* Brenan and *rostrata* Brenan
A. tucumanensis Griseb.
A. villosa (Sw.) Willd.
A. visco Griseb.
A. visite Griseb. = *A. visco*
A. welwitschii Oliv. subsp. *delagoensis* (Harms) J. Ross & Brenan

Nodulated members of sub-genus Phyllodineae

A. acinacea Lindl.
A. acuminata Benth.
A. adsurgens Maiden
A. adunca A. Cunn.
A. alata R. Br.
A. amoena Sieb. Wendl
A. ampliceps Maslin
A. aneura Benth.
A. armata R. Br. = *A. paradoxa*
A. aspera Lindl.
A. auriculiformis (Benth. = *auriculaeformis*
A. baileyana F. Muell.
A. binervata DC.
A. binervia (Wendl.) Macbr.
A. bidentata Benth.
A. biflora R. Br.
A. bivenosa DC.
A. blakelyi Maiden
A. brachybotrya Benth.
A. brachystachya Benth.
A. buxifolia Cunn.
A. burrowi Maiden
A. bynoeana Benth.
A. calamifolia Lindl.
A. cambagei R.T. Baker
A. cana Maiden
A. cangaiensis Tind. & Kodela
A. cardiophylla Benth.
A. celastrifolia Benth.
A. cincinnata F. Muell.
A. cognata Domin.
A. colletioides (A. Cunn.) Benth.
A. cometes Andrews
A. complanata Benth.
A. concurrens L. Pedley
A. confusa Merr.
A. cultriformis G. Don
A. cunninghamii Hook. = *A. concurrens*
A. cyanophylla Lindl. = *A. rostellifera*
A. cyclops A. Cunn. ex G. Don.
A. deanei (R.T. Baker) Welch, Coombe & McGlynn
A. dealbata Link
A. decora Reichb. F.
A. decurrens Willd. (P)
A. dimidiata Benth.
A. diptera Lindl.
A. discolor (Lam.) Willd.
A. doratoxylon Cunn.
A. drummondii Lindl.
A. elata Benth.
A. elongata Sieb. ex DC.
A. eremophylla Fitzg.
A. ericifolia Benth. = *A. ericaefolia*
A. erinacea Benth.
A. esterhazia MacKay
A. estrophiolata F. Muell.
A. extensa Lindl.
A. falcata Willd.
A. filicifolia Cheel & Welch
A. filifolia Benth.
A. fimbriata G. Don
A. flexifolia Benth., A. McInnes & J. Brockwell, pers. comm. (2008)
A. floribunda (Vent.) Willd.
A. fulva Tind.

A. genistifolia Link, A. McInnes & J. Brockwell, pers. comm. (2008)
A. genistoides (F. Muell.) Benth.
A. georginae Bailey
A. gittinsii L. Pedley
A. gladiiformis Benth.
A. glaucescens Willd.
A. glaucocarpa Maiden & Blakely
A. glaucoptera Benth.
A. granitica Maiden
A. hakeoides Benth.)
A. harpophylla Benth.
A. harveyi Benth.
A. hastulata Sm.
A. hilliana Maiden
A. heterophylla (Lam.) Willd.
A. hippuroides = *longipedunculata*
A. homalophylla Benth.
A. holosericea G. Don
A. horridula Meisn.
A. huegelii Benth.
A. implexa Benth.
A. irrorata Spreng.
A. iteaphylla Benth.
A. jonesii Muell. & Maiden
A. juncifolia Benth
A. juniperiana Willd.
A. kauaiensis Hillebrand
A. kempeana F. Muell.
A. koa A Gray and vars. *hawaiiensis* Rock and *lanaiensis* Rock
A. koaia Hillebrand
A. latifolia Benth.
A. leptocarpa A. Cunn. ex Benth.
A. leiocalyx (Domin.) L. Pedley
A. leptoneura Benth.
A. leucoclada Tind.
A. ligulata A. Cunn.
A. linearis Sims
A. lineata G. Don
A. longifolia (Andrews) Willd. and vars. *floribunda* F. Muell., and *sophorae* F.
A. lunata Sieb.
A. lysiphloia F. Muell.
A. mangium Willd.
A. mearnsii De Wild.
A. melanoxylon R. Br.
A. microbotrya Benth.
A. monticola Brenan & Exell = *A. montigena*
A. mooreana Fitzg.
A. mountfordea Specht
A. myrtifolia Willd.
A. nanodealbata J.H. Willis
A. neriifolia Benth.
A. nervosa DC.
A. nigricans R. Br.
A. notabilis F. Muell.
A. obliqua Benth.
A. obliquinervea Tind.
A. obscura DC.
A. oswaldii F. Muell.
A. oxycedrus Sieb.
A. papyrocarpa Benth.
A. paradoxa DC. as *A. armata*
A. parvipinnula Tind.
A. paramattensis Tind.
A. pendula G. Don
A. pentadenia Lindl.
A. platycarpa F. Muell.
A. podalyriifolia G. Don = *A. podalyriaefolia*
A. pravissima F. Muell.
A. prominens G. Don
A. pulchella R. Br.
A. pumila Maiden
A. pycnantha Benth.
A. pyrifolia DC.
A. retinodes Schldl.
A. restiacea Benth.
A. richii A. Gray
A. rigens G. Don
A. rostellifera Benth., as *A. cyanophylla*
A. rothii F.M. Bailey
A. salicina Lindl.
A. rossei F. Muell. A. McInnes pers. comm. (2007)
A. rubida Cunn.
A. salicina Lindl., McInnes & Brockwell, pers. comm. (2008)
A. saligna (Labill.) Wendl.
A. shirleyi Maiden
A. sophorae (Labill.) R. Br.
A. spinescens Benth.
A. spinosissima Benth A. McInnes, pers. comm. (2007)
A. squamata Lindl.
A. stenoptera Benth.
A. stricta (Andrews) Willd.
A. strigosa Link
A. suaveolens (Smith) Willd.
A. subcaerulea Lindl.
A. sulcata R. Br.
A. terminalis (Salisb.) J.F. McBride
A. tamminensis Pritz.
A. trachycarpa Pritz.
A. trachyphloia Tind.
A. translucens A. Cunn.
A. triptera Benth.
A. ulicifolia (Salisb.) Court var. *brownei* (Poir.) L. Pedley
A. uncifera Benth.
A. urophylla Benth.
A. verniciflua Cunn.
A. vestita Ker Gawler
A. verticillata (L'Her.) Willd.
A. victoriae Benth.
A. volubilis F. Muell.

Albizia

A. acle (Blanco) Merr.
A. adianthifolia (Schum.) W. Wight
A. adinocephala (J.D. Smith) Rec. as *Pithecellobium adinocephalum* Donn. Smith
A. altisisima Hook f. Diabate et al. (2005)
A. amara (Roxb.) Boivin subsp. *sericocephala* (Benth.) Brenan
A. anthelmintica Brongn.
A. antunesiana Harms
A. berteriana (DC.) M. Gomez, as *Acacia berteriana*
A. brevifolia Schinz.
A. carbonaria Britton
A. chevalieri Harms.

A. chinensis (Osbeck) Merr.
A. coriaria Welw. ex Oliv.
A. corymbosa (L.C. Rich.) G.P. Lewis & P.E. Owen = *Hydrochorea corymbosa*
A. decandra (Ducke) Barneby & Grimes
A. dinklagei (Harms) Harms Diabate et al. (2005)
A. distachya (Vent.) Macbr. = *Paraserianthes lophantha* (Willd.) Nielsen
A. ealensis De Wild. = *A. gummifera* var. *ealensis* (De Wild.) Brenan
A. edwallii (Hoehne) Barneby & Grimes, as *Pithecellobium edwallii* Hoehne
A. elegans (Ducke) L. Rico, as *Balizia elegans* (Ducke) Barneby & J.W. Grimes, S.M. de Faria pers. comm. to J.H. Kirkbride (2006)
A. falcata (L.) Backer = *Paraserianthes falcataria* (L.) Nielsen now in *Falcataria*
A. forbesii Benth.
A. glaberrima (Schum. & Thonn.) Benth. var *glabrescens* (Oliv.) Brenan
A. guachapele (Kunth) Dugand = *Pseudosmanea guachapele*
A. gummifera (J. Gmelin) C.A. Smith
A. harveyi Fourn.
A. inopinata (Harms) G.P. Lewis = *Samanea inopinata*
A. inundata (Mart.) Barneby & J.W. Grimes
A. julibrissin Durazz.
A. kalkora (Roxb.) Prain Wang et al. (2006)
A. katangensis Willd. = *A. coriaria*
A. lebbek (L.) Benth.
A. lebbekoides (DC.) Benth.
A. leptophylla Harms
A. lophantha (Willd.) Benth. = *Paraserianthes lophantha* (Willd.) Nielsen
A. lucidior (Steud.) I. Nielsen, as *A. lucida* (Roxb.) Benth., *A. moluccana* (Willd.) Benth. = *Falcataria moluccana* (Miq.) Barneby & Grimes
A. multiflora var. *multiflora* (Kunth.) Braneby & J.W. Grimes
A. niopoides (Benth.) Burk.
A. occidentalis Brandegee Altimarino-Hernández et al. (2004) = *Hesperalbizia occidentalis*
A. odoratissima (L.f.) Benth.
A. pedicellaris (DC.) L. Rico, as *Balizia pedicellaris*
A. petersiana subsp *evansii* (Burtt Davy) Brenan
A. polycephala (Benth.) Rec.
A. polyantha (Spreng.) G.P. Lewis = *A. inundata* (Mart.) Barneby & Grimes
A. polycephala (Benth.) Killip
A. procera (Roxb.) Benth.
A. retusa Benth.
A. saponaria (Lour.) Miq.
A. sassa (Willd.) Macbr. = *A. adianthifolia*
A. schimperana Oliv. vars *amaniensis* (Baker f.) Brenan, *schimperana* Oliv. now spelled *A. schimperiana*
A. suluensis Gerstner
A. tanganyicensis Baker f.
A. versicolor Welw. ex Oliv.
A. zimmermannii Harms
A. zygia (DC.) J.F. Macbr.

Anandenanthera

A. peregrina (L.) Speg.
A. falcata (Benth.) Speg. = *A. peregrina* (L.) Speg. var *falcata* (Benth.) Altschul

Archidendron

A. bigemina (L.) I.C. Nielsen
A. clypearia (Jack) I.C. Nielsen
A. ellipticum (Blume) I.C. Nielsen
A. kanisii R.S. Cowan
A. scutiferum (Blanco) I.C. Nielsen
A. utile (Chun & F.C. How) I.C. Nielsen. Ng & Hau (2009)

Archidendropsis

A. basaltica (F. Muell.) I.C. Nielsen
A. thozetiana (F. Muell.) I. Nielsen

Calliandra

C. acapulcensis (Britton & Rose) Standl. = *C. houstiana* var. *acapulcensis*
C. affinis Pittier = *C. cruegeri*
C. brevipes Benth., as *C. selloi*
C. calothyrsus Meisn.
C. coriacea (Willd.) Benth. Diabate et al. (2005)
C. cruegeri Griseb.
C. eriophylla Benth.
C. erubescens Renv.
C. foliolosa Benth.
C. grandiflora (L'Her.) Benth. = *C. houstoniana* (Mill.) Standl. var. *anomala* (Kunth) Barneby
C. guildingii Benth.
C. haematocephala Hassk.
C. haematomma Benth.
C. harrisii (Lindl.) Benth.
C. houstoniana (Miller) Standl.
C. inaequilatera Rusby = *C. haematocephala* var. *haematocephala* Hassk.
C. juzepczukii Standl.)
C. longipedicellata Macqueen & H.M. Hern. James et al. (2007) unpub
C. macrocalyx Harms
C. parviflora Benth.

C. physocalyx H.M. Hern. & M. Sousa. James et al. (2007) unpub.
C. pitteri Standl. Diabate et al. (2005)
C. rubescens (M. Martens & Galeotti) Standl. James et al. (2007) unpub.
C. selloi (Spreng.) Macbr. = *C. brevipes*
C. surinamensis Benth.
C. tenuiflora Benth.) = *C. surinamensis*
C. tergeminia var. *emarginata* (Humb. & Bonpl. ex Willd.) Barneby
C. trinerva var *arborea* James et al. (2007) unpub.
C. tweediei Benth.

Cedrelinga

C. cateneformis (Ducke) (also spelled *catenaeformis*)

Chloroleucon

C. dumosum (Benth.) G.P. Lewis
C. foliolosum (Benth.) G.P. Lewis, as *Pithecellobium foliolosum* Benth.
C. mangense (Jacq.) Britton & Rose, and var. *vincentis* (Benth.) Barneby & Grimes, as *Pithecellobium caraboense* Harms
C. tortum (Mart.) Pittier, as *Pithecellobium tortum* Mart.

Cojoba

C. arborea (L.) Britton & Rose var. *arborea*

Desmanthus

D. brachylobus Benth. = *D. illinoensis*
D. illinoensis (Michx.) Macmillan
D. leptolobus Torr. & A. Gray
D. velutinus Scheele
D. virgatus (L.) Willd.

Dichrostachys

D. cinerea (L.) Wight & Arn. This species has been divided into a series of subspp. each of which may have several vars. The following subspp. (and in some cases vars. within them) have been reported as nodulated, *africana* (Brenan & Brummitt, *argillicola* Brenan & Brummitt, *cinerea* (L.) Wight & Arn., *nyassana* (Taub.) Brenan, *platycarpa* (W. Bull) Brenan & Brummitt, *D. spicata* (F. Muell.) Domin.

Ebenopsis

E. confinis (Standl.) Britton & Rose
E. ebana (Berland) Barneby & J.W. Grimes

Elephantorrhiza

E. burkei Benth.
E. elephantina (Burchell) Skeels
E. goetzei subsp. *goetzei* (Harms) Harms
E. suffruticosa Schinz

Entada

E. abyssinica A. Rich.
E. africana Guill. & Perr. Diabate et al. (2005)
E. arenaria Schinz
E. chrysostachys (Benth.) Drake
E. gigas (L.) Fawc. & Rendle Diabate et al. (2005)
E. mannii (Oliv.) Tisser
E. phaseoloides (L.) Merr.
E. polyphylla Benth.
E. polystachya (L.) DC.
E. rheedei subsp. *sinohimalensis* (Grierson & D.G. Long) Panigrahi

Enterolobium

E. contortisiliquum (Vell.) Morong. This is sometimes taken as a synonym of *E. timbouva*, although both species are recognised by Barneby & Grimes (1996).
E. cyclocarpum (Jacq.) Griseb.
E. ellipticum Benth.
E. gummiferum (Mart.) Macbr.
E. maximum Ducke
E. monjollo (Vell.) Mart.
E. schomburgkii Benth.
E. timbouva Mart.

Faidherbia

F. albida (Del) A. Chev.

Falcataria

F. moluccana (Miq.) Barneby & Grimes, as *Paraserianthes falcataria* (L.) Nielsen

Havardia

H. confinis (Standl.) Britton & Rose = *Ebenopsis confinis*
H. mexicana (Rose) Britton & Rose
H, pallens (Benth.) Britton & Rose

Hesperalbizia

H. occidentalis (Brandegee) Barneby & Grimes

Hydrochorea

H. corymbosa (Rich.) Barneby & Grimes, as *Pithecellobium corymbosum* (Rich.) Benth.
H. gonggrijpii (Kunth) Barneby & J. W. Grimes S.M. de Faria pers. comm. to J.H. Kirkbride (2006)
H. marginata (Kleinh.) Barneby & J.W. Grimes var. *marginata* S.M. de Faria pers. comm. to J.H. Kirkbride (2006)

Inga

I. acreana Harms, as *I. acreanum*
I. acrocephala Steud.
I. acuminata Benth. S.M. de Faria, pers. comm. to J.H. Kirkbride (2006)
I. affinis DC. = *I. vera* subsp. *affinis* (DC.) T.D. Penn.
I. alba (Sweet) Willd.
I. aptera (Vinha) T.D. Penn.
I. bahiensis Benth., as *Affonsea bahiensis*
I. blanchetiana Benth.
I. calantha Ducke
I. capitata Desv.
I. cayenensis Benth.
I. chocoensis Killip ex T.S. Elias
I. cinnamomea Benth.
I. congesta T.D. Penn.
I. cordistipulata Mart.
I. disticha Benth.
I. duckei Huber Diabate et al. (2005)
I. edulis Mart.
I. fagifolia (L.) Benth. = *I. laurina* (Sweet) Willd.
I. fanchoniana O. Poncy
I. fastuosa (Jacq.) Willd.
I. fuelleei DC. Grossman (2005)
I. graciliflora Benth.
I. gracilifolia Ducke
I. hayesii Benth. Parker (2003)
I. heterophylla Willd.
I. hispida Benth.
I. huberi Ducke
I. ingoides (Rich.) Willd.
I. jenmaii Sandw.
I. jiniciul G. Don
I. lateriflora Miq. (= *I. laterifolia* Miq. of Allen & Allen ?).
I. laurina (Sw.) Willd.
I. leiocalycina Benth.
I. lentiscifolia Benth. as *I. lenticifolia*
I. lomatophylla Benth.
I. luschnathiana Benth. = *I. subnuda* subsp. *luschnathiana* (Berth.) T.D. Penn.
I. macrophylla Willd.
I. marginata Willd. = *I. semialata*
I. maritima Benth.
I. meissneriana Miq. = *I. vera* subsp. *affinis* (DC.) T.D. Penn.
I. microcalyx Spruce ex Benth. S.M. de Faria, pers. comm. to J.H. Kirkbride, (2006)
I. mortoniana J. Léonard
I. nobilis Willd.
I. nuda Benth. = *I. striata*
I. oerstediana Benth.
I. ornata Kunth
I. paraensis Ducke
I. paterno Harms = *I. jinicuil*
I. pavoniana G. Don Grossman (2005)
I. pezizifera Benth.
I. pilosula (Rich.) Macbr., as *I. setifera*
I. puncata Willd.
I. rubiginosa (Rich.) DC.
I. sapindoides Willd.
I. sarmentosa Glaziou
I. semialata (Vell. Conc.) C. Mart.
I. setifera DC. = *I. pilosula*
I. spectabilis (Vahl) Willd.
I. splendens Willd.
I. stipularis DC.
I. striata Benth.
I. subnuda Salzm.
I. thibaudiana DC.
I. tubaeformis Benoist
I. umbratica Poepp. & Endl. S.M. de Faria, pers. comm. to J.H. Kirkbride (2006) = *I. umbellifera*
I. umbellifera (Vahl) Steud. ex DC.
I. uraguensis Hook. & Arn. = *I. vera* subsp. *affinis* (DC.) T.D. Penn.
I. venosa Griseb.
I. velutina Willd. S.M. de Faria, pers. comm to J.H. Kirkbride (2006)
I. vera Willd.
I. vuplina Mart ex Benth.

Leucaena

L. collinsii Britton & Rose
L. cuspidata Standl.
L. esculenta (DC.) Benth.
L. glabrata Rose = *L. leucocephala*
L. greggii S. Watson
L. involucrata Zarate
L. lanceolata S. Watson
L. lempirana C.E. Hughes
L. leucocephala (Lam.) de Wit
L. magnifica (C.E. Hughes) C.E. Hughes
L. matudae (Zarate) C.E. Hughes
L. multicapitula Scherv. as collinsii
L. pallida Britton & Rose
L. pulverulenta (Schltdl.) Benth. as collinsii
L. salvadorensis Standl. ex Britton & Rose
L. shannonii Donn. Sm.
L. trichandra (Zucc.) Urb.
L. trichodes (Jacq.) Benth.

Lysiloma

L. divaricatum (Jacq.) Macbr.
L. latisiliquum (L.) Benth.

L. microphylla Benth. = *L. divaricatum*
L. tergemina Benth.)
L. watsonii Rose, as *L. thornberi* Britton & Rose

Macrosamanea

M. discolor (Willd.) Britton & Killip, var *discolor*, formerly *Pithecellobium adiantifolium* (Kunth.) Benth.
Macrosamanea duckei (Huber) Barneby & J. W. Grimes, S.M. de Faria pers. comm. to J.H. Kirkbride (2006)
M. pubiramea (Steud.) Barneby & Grimes and var. *lindsaeifolia* = *P. lindsaeifolium* Spruce ex Benth.

Microlobius

M. foetidus (Jacq.) M. Sousa & G. Andrade, subsp. *paraguensis* (Benth.) M. Sousa & G. Andrade, as *Goldmania paraguensis*

Mimosa

M. acanthocarpa Poir. = *M. aculeaticarpa* Ortega
M aculeaticarpa Ort. var *aculeaticarpa* Elliott et al. (2007a)
M. acutistipula Benth.
M. adenocarpa Benth. Elliott et al. (2007a)
M. affinis Robinson
M. albida H&B. ex Willd. var *albida* Elliott et al. (2007a)
M. albida H&B. ex Willd. var *strigosa* Elliott et al. (2007a)
M. albida var *willdenowii* (Poir.) Rudd, as *M. floribunda* Willd.
M. albolanata Taub. James et al. (2007) unpub.
M. aparidensis Burk. (assumed to be the species given as *M. aparacina* Burk.)
M. arenosa (Willd.) Poir.
M. artemisiana Heringa & Paula
M. bahamensis Benth.)
M. benthamii Macbr. var *malacocarpa* (B.L. Rob.) J.F. Macbride (James et al., (2007)) unpub.
M. bimucronata (DC.) Kuntze
M. biuncifera Benth. = *M. aculeaticarpa*
M. blanchetii Benth.
M. barchycarpa Benth.
M. borealis A. Gray Elliott et al. (2007a)
M. caesalpinifolia Benth.
M. callithrix Malme James et al. (2007) unpub.
M. calodendron Mart.
M. campicola Harms var planiges Barneby M. Simon pers. comm. (2007)
M. camporum Benth.
M. casta L.
M. ceratonia L.M. Simon (2007)
M. claussenii Benth. James et al. (2007) unpub.
M. cordistipula Benth James et al. (2007) unpub.
M. crumenarioides L.P. Queiroz & G.P. Lewis, M. Simon pers. comm. (2007)
M. cyclophylla Taub. James et al. (2007) unpub.
M. decorticans Berneby James et al. (2007) unpub.
M. debilis Willd.
M. delicatula Baill. Elliott et al. (2007a)
M. densa Benth. James et al. 2007 unpub.
M. depauperata Benth. James et al. (2007) unpub
M. discoloba Barneby James et al. (2007) unpub.
M. dolens Vell. Conc.
M. dominarum Barneby James et al. (2007) unpub.
M. dormiens Willd.
M. dysocarpa A. Gray
M. filipes Martius
M. flocculosa Burkart
M. floribunda Willd. = *M. albida* var. *willdenow*
M. filipetiola Burkart Lammel et al. (2007)
M. foliolosa Benth. James et al. (2007) unpub.
M. furfuracea Benth. Lammel et al. (2007)
M. gardneri Benth. James et al. (2007) unpub.
M. gemmulata Barneby James et al. (2007) unpub.
M. gracilis Benth. James et al. (2007) unpub.
M. guilandinae (DC.) Barneby and var *spruceana* (Benth.) Barneby Faria pers. comm. to J.H. Kirkbride (2006)
M. hamata Willd.
M. hexandra Micheli Elliott et al. (2007a)
M. himalayana Gamble Elliott et al (2007a)
M. hirsutissima Mart. James et al. (2007) unpub.
M. hondurana Britt. M. Simon, pers. comm.
M. humivagans Barneby James et al. (2007) unpub.
M. hypoglauca Mart. James et al. (2007) unpub.
M. invisa Colla
M. irrigua Barneby James et al. (2007) unpub.
M. lacerata Rose James et al. (2007) unpub
M. lactiflua Delile ex Benth. James et al. (2007) unpub.
M. laniceps Barneby James et al. (2007) unpub.
M. lanuginosa Burkart James et al. (2007) unpub.

M. laticifera Rizz. & Mattos = *M. obovata*
M. latispinosa Lam. Elliott et al. (2007a)
M. lewisii Barneby James et al. (2007) unpub.
M. luisana Brandegee
M. manidea Barneby James et al. (2007) unpub.
M. melanocarpa Benth. James et al. (2007) unpub.
M. menabeensis R. Vig. Elliott et al. (2007a)
M. mensicola Barneby
M. mollis Benth. James et al. (2007) unpub.
M. monancistra Benth. James et al. (2007) unpub
M. myriadena (Benth.) Benth. Faria pers. comm. to J.H. Kirkbride (2006)
M. nuda Benth. James et al. (2007) unpub.
M. obovata Benth., as *M. laticifera*
M. occidentalis Britton & Rose, var *occidentalis* M. Simon, pers. comm. (2008)
M. ophthalmocentra Benth.
M. orthocarpa Benth.
M. pellita Willd.
M. pigra L.
M. pilulifera Benth. and var *pseduincana* (Burk.) Barneby Lammel et al. (2007)
M. polyantha Benth.
M. polycarpa Kunth
M. polydactyla Willd., as *M. polydactyla* Humb. & Bonpl.
M. polystachya Kunth = *Entada polystachya*
M. pseudoradula Glaz. ex Barneby James et al. (2007) unpub.
M. pseudosepiaria Harms James et al. (2007) unpub.
M. pteridifolia Benth. James et al. (2007) unpub.
M. pudica L.
M. pyrenea Taub. James et al. (2007) unpub.
M. quadrivalvis L. var. *leptocarpa* (DC.) Barneby, as *Schrankia leptocarpa*, and var. *angustata* (Torr. & A. Gray) Barneby, as *Schrankia uncinata*
M. regina Barneby James et al. (2007) unpub.
M. robusta R. Grether M. Simon, pers. comm. (2008)
M. rufescens Benth. Faria pers comm to J. H. Kirkbride (2006)
M. scabrella Benth.
M. sensibilis Griseb.
M. setosa Benth. var. *paludosa* (Benth.) Barneby
M. setosissima Taub. James et al. (2007) unpub.
M. setuligera Harms. James et al. (2007) unpub.
M. skinneri Benth. James et al. (2007) unpub.
M. somnians Willd., as *M. somnians* Humb. & Bonpl.
M. speciosissima Taub. James et al. (2007) unpub.
M. splendida Barneby James et al. (2007) unpub.
M. strigillosa Torr. & A. Gray
M. tenuiflora (Willd.) Poir., as *M. tenuiflora* Benth.
M. tequilana S. Watdon James et al. (2007) unpub
M. thermarum Barneby James et al. (2007) unpub.
M. tomentosa Willd., as *M. tomentosa* Hunb. & Bonpl.
M. tricephalq Cham. & Schitl. var *tricephala* James et al. (2007) unpub.
M. ulbrichinana Harms. James et al. (2007) unpub.
M. ulei Taub. James et al. (2007) unpub.
M. uliginosa Chodat & Hassl.
M. ursina Mart. James et al. (2007) unpub.
M. uruguensis Hook. & Arn. Elliott et al. (2007a)
M. velloziana Mart.
M. venatorum Barneby James et al. (2007) unpub.
M. verecunda Benth. James et al. (2007) unpub.
M. verrucosa Benth.
M. vestita Benth. James et al. (2007) unpub.
M. xanthocentra Mart.
M. zimapanensis Britton & Rose = *M. tenuiflora*

Mimozyganthus

Mimozyganthus carinatus (Griseb.) Burkart.

Neptunia

N. gracilis Benth.
N. lutea (Leavenw.) Benth.
N. monosperma F. Muell.
N. natans (L.f.) Druce = *N. oleracea*
N. plena (L.) Benth.
N. pubescens Benth.

Parapiptadenia

P. excelsa (Griseb.) Burkart
P. pterosperma (Benth.) Brenan
P. rigida (Benth.) Brenan

Paraserianthes

P. lophantha (Willd.) Nielsen

Pentaclethra

P. macroloba (Willd.) Kuntze

Piptadenia

P. adiantoides (Spreng.) Macbr.
P. constricta Micheli Altamirano-Hernandez et al. (2004) = *Pityrocarpa obliqua*

P. flava (Spreng. ex DC.) Benth.
P. gonoacantha (Mart.) Macbr.
P. moniliformis Benth. = *Pityrocarpa moniliformis* (Benth.) Luckow & Jobson
P. paniculata Benth.
P. stipulacea (Benth.) Ducke
P. viridiflora (Kunth) Benth.) now in a new, unnamed genus

Piptadeniastrum

P. africanum (Hook. f.) Brenan

Pithecellobium

P. diversifolium Benth.
P. dulce (Roxb.) Benth.
P. ellipticum (Blume) Hassk. = *Archidendron ellipticum*
P. hymenaeafolium (Willd.) Benth. Barrett & Parker (2005)
P. lanceolatum (Willd.) Benth.
P. platycarpum Merr. as *P. platylobium* González-Ruiz et al. (2008)
P. racemosum Ducke = *Zygia racemosa*
P. unguis-cati (L.) Benth.

Pityrocarpa

P. moniliformis (Benth.) Luckow & Jobson as *Piptadenia moniliformis*
P. obliqua (Pers.) J. F. Macbr., as *Piptadenia obliqua*

Plathymenia

P. foliolosa Benth. now included in *P. reticulata*, Warwick & Lewis (2003).
P. reticulata Benth.

Prosopis

P. affinis Spreng.
P. africana (Guill. & Perr.) Taub.
P. alba Griseb.
P. articulata S. Watson
P. chilensis (Molina) Stunz
P. cineraria (L.) Druce)
P. dulcis Kunth = *P. laevigata*
P. farcta (Banks & Sol) J.F. Macbr
P. ferox Griseb
P. flexuosa DC.
P. glandulosa Torr., as *P. juliflora* var. *glandulosa*
P. juliflora (Sweet) DC.
P. kuntzei Kuntze
P. laevigata (Willd.) M. Johnst., as *P. dulcis*
P. nigra (Griseb.) Hieronymus
P. pallida (Willd.) Kunth
P. pubescens Benth
P. ruscifolia Griseb.
P. stephaniana (Willd.) Spreng = *P. farcta*
P. tamarugo Phil.
P. velutina Woot.
P. vidaliana Fernandez-Villar = *P. juliflora*

Pseudopiptadenia

P. contorta (DC.) G.P. Lewis & M.P. Lima
P. psilostachya (DC.) G.P. Lewis & M.P. Lima

Pseudosamanea

P. guachepele (Kunth) Harms

Samanea

S. inopinata (Harms) Barneby & Grimes, as *Pithecellobium inopinatum* Harms
S. saman (Jacq.) Merr.

Schleinitzia

S. fosbergii Nevlung & Niezgoda
S. insularum (Guill.) Burkart, as *Leucaena insularum*

Serianthes

S. inopinata Harms
S. myriadenia (Guill.) Benth. S.M. de Faria pers. comm. to J.H. Kirkbride (2006)

Stryphnodendron

S. adstringens (Mart.) Cov.
S. barbadetimam Mart. = *S. adstringens*
S. guianense (Aubl.) Benth.
S. paniculatum Poepp. & Endl. S.M. de Faria pers. comm. to J.H. Kirkbride (2006)
S. polystachyum (Miq.) Kleinhoonte
S. pulcherrimum (Willd.) Hochr.
S. racemiferum (Ducke) W. Rodrigues

Wallaceodendron

W. celebicum Koord.

Xerocladia

X. viridiramis (Burchell) Taubert.

Zygia

Z. cataractae (Kunth.) L. Rico
Z. cauliflora (Willd.) Killip, as *Pithecellobium cauliflorum* Mart.
Z. claviflora (Benth.) Barneby & Grimes, as *Pithecellobium claviflorum* Benth. = *Z. latifolia* var. *Communis* Barneby &. Grimes

Z. collina (Sandwith) Barneby & Grimes, as *Pithecellobium collinum* Sandwith
Z. glomerata (Pittier) Pittier, as *Z. glomerata* (DC.) Pittier
Z. inaequalis (Willd.) Pittier, as *Z. inaequalis* (Humb. & Bonpl.) Pittier
Z. juruana (Harms) L. Rico
Z. latifolia (L.) Fawcett & Rendle, as *Pithecellobium latifolium* Benth. and var var. *lasiopus* (Benth.) Barneby & J. W. Grimes S.M. de Faria pers. comm. to J.H. Kirkbride (2006)
Z. racemosa (Ducke) Barneby & Grimes
Z. ramiflora (F. Muell.) Kosterm. S.M. de Faria pers. comm. to J.H. Kirkbride (2006)
Z. sanguinea (Benth.) L. Rico, as *Pithecellobium* (*Zygia*) *sanguineum* Benth. = *Z. selloi*
Z. selloi (Benth.) L. Rico

Appendix III: Papilionoideae

Abrus

A. canescens Baker Diabate et al. (2005)
A. fruticulosus sensu Torre = *A. pulchellus* subsp. *suffruticosus* (Boutique) Verdc.
A. laevigatus E. Mey.
A. precatorius L.
A. pulchellus Thwaites and var. *tenuiflorus* (Benth.) Verdc., as *A. stictosperma*
A. schimperi Baker
A. stictosperma Berhaut = *A. pulchellus* var. *tenuiflorus*

Acmispon

A. parviflorus (Benth.) D.D. Sokolov, as *Hosackia parviflora.* Also known as *Lotus macranthus.*
A. wrangelianus (Fisch. & C.A. Mey.) D.D. Sokoloff, as *Lotus wrangelianus*

Acosmium

A. bijugum (Vogel) Yalovlev
A. nitens (Vogel) Yakovlev
A. praeclarum (Sandwith) Yakovlev, as *Sweetia praeclara* Sandwith

Adenocarpus

A. complicatus (L.) Gay
A. decorticans Boiss.
A. foliolosus DC.

Adenodolichos

A. punctatus (Micheli) Harms

Adesmia

A. bicolor (Poir.) DC.
A. capitellata (D. Clos) Hauman
A. glomerula var. *glomerula* D. Clos
A. latifolia (Spreng.) Vogel
A. muricata (Jacq.) DC.
A. punctata (Poir.) DC.
A. retusa Griseb.

Aeschynomene

A. abyssinica (A. Rich.) Vatke
A. afraspera J. Léonard
A. americana L.
A. aphylla Wild
A. bracteosa Baker
A. brasiliana (Poir.) DC. var. *brasiliana* (Poir.) DC.
A. ciliata Vogel
A. crassicaulis Harms
A. cristata Vatke
A. denticulata Rudd
A. elaphroxylon (Guill. & Perr.) Taub.
A. evenia C. Wright vars. *evenia* C. Wright and *serrulata* Rudd
A. falcata (Poir.) DC.
A. filosa Mart.
A. fluitans Peter
A. fluminensis Vell.
A. fulgida Baker
A. gazensis Baker f.
A. grandistipulata Harms
A. histrix Poir. vars. *histrix* Poir. and *incana* (Vogel) Benth.
A. indica L.
A. inyangensis Wild
A. lateritia Harms
A. laxiflora Bojer
A. mediocris Verdc.
A. megalophylla Harms
A. micranthos (Poir.) DC.
A. mimosifolia Vatke
A. minutiflora Taub.
A. nilotica Taub.
A. nodulosa (Baker) Baker f. and vars. *glabrescens* Gillett and *nodulosa* (Baker) Baker f.
A. nyassana Taub.
A. paniculata Vogel
A. pfundii Taub.
A. pratensis Small
A. portoricensis Urb.
A. pulchella Baker

A. rehmannii Schinz and var. *leptobotrya* (Harms) Gillett Diabate et al. (2005)
A. rhodesiaca Harms
A. rudis Benth.
A. scabra G. Don
A. schimperi A. Rich.
A. schliebenii Harms
A. sensitiva Sw.
A. tambacoundensis Berhaut
A. trigonocarpa Baker f.
A. uniflora E. Mey.
A. villosa Poir.
A. viscidula Michx.

Aganope

A. gabonica (Baill.) Polhill, as *Ostryoderris gabonica* (Baill.) Dunn

Alhagi

A. maurorum Medik., also as *A. camelorum* Fisch.
A. sparsifolia Shap.

Alistilus

A. bechuanus N.E. Br.

Alysicarpus

A. belgaumensis W. Wight
A. bupleurifolius (L.) DC.
A. glumaceus (Vahl) DC.
A. heterophyllus (Baker) Jafri & Ali
A. longifolius Wight & Arn.
A. ludens Wall.
A. monilifera DC.
A. ovalifolius (Schum.) J. Léonard
A. pubescens Y.W. Law ex Wight
A. rugosus Willd.) DC. and subspp. *perennirufus* J. Léonard and *rugosus* (Willd.) DC.
A. scariosus (Spreng) Thwaites
A. tetragonolobus Edgew.
A. vaginalis (L.) DC.
A. zeyheri Harv.

Amicia

A. micrantha Kuntze T Sarkinin pers. comm. (2007)
A. medicaginea Griseb. T Sarkinin pers. comm. (2007)
A. andicola (Griseb.) Harms T Sarkinin pers. comm. (2007)

Ammopiptanthus

A. mongolicus (Kom.) S.H. Cheng

Amorpha

A. californica Torr. & A. Gray
A. canescens Pursh
A. elata Bouché
A. fragrans Hort. = *A. fruticosa*
A. fruticosa L.
A. glabra Poir., assumed to = *A. glabra* Desf. recorded in Allen & Allen (1981)
A. herbacea Walter
A. microphylla Pursh = *A. nana*
A. nana Fraser

Amphicarpaea

A. bracteata (L.) Fern. and subsp. *edgeworthii* Benth., as *A. edgeworthii.*
A. edgeworthii Benth. = *A. bracteata*, subsp. *edgeworthii* (Benth.) H. Ohashi
A. trisperma Baker

Amphithalea

A. intermedia Eckl. & Zeyh.
A. ericifolia (L.) Eckl. & Zeyh.
A. parvifolia (Thunb,) A.L. Schutte

Anagyris

A. foetida L.
A. latifolia Brouss. ex Willd.

Andira

A. anthelmia (Vell. Conc.) J.F. Macbr.
A. coriacea Pulle
A. fraxinifolia Benth.
A. frondosa Benth.
A. inermis (Wright) DC.
A. legalis (Vell. Conc.) Tol.
A. nitida Benth.
A. pisonis Mart.
A. racemosa Lam.
A. surinamensis (Bondt) Pulle

Anthyllis

A. barba-jovis L.
A. cornicina L., = *Hymenocarpos cornicina*
A. cytisoides L.
A. henoniana Batt.
A. jaquinii Kerner = *A. montana* subsp. *jacquinii*
A. lotioides L., = *Hymenocarpos lotioides*
A. macrocephala Wend. = *A. vulneraria* subsp. *polyphylla* (DC.) Nyman
A. montana L. and subsp. *jacquinii* (A. Kerner) Hayek, as *A. jacquinii*
A. polyphylla Kit. = *A. vulneraria* subsp. *polyphylla*
A. tetraphyllis L. = *Tripodion tetraphyllum*
A. vulneraria L. and subsp. *polyphylla* (DC.) Nyman, as *A. polyphylla*

Antopetitia

A. abyssinica A. Rich.

Aotus

A. ericoides (Vent.) G. Don
A. lanigera Cunn.
A. preissii Meisn.
A. tietkinsii F. Muell.
A. villosa (Andrews) Smith = *A. ericoides*

Apios

A. americana Medik
A. carnea (Wall) Benth. ex Baker.

Aphyllodium

A. biarticulatum (L.) Gagnep. as *Dicerma biarticulatum* (L.) DC.

Arachis

A. batizocoi Krapov & W.C. Greg
A. burkartii Handro
A. cardenasii Krapov & W.C. Greg
A. diogoi Hoehne
A. duranensis Krapov & W.C. Greg
A. glabrata Benth. and var. *hagenbeckii* (Harms) Hermann
A. halodes Mart. ex Krapov & Rigoni
A. hypogaea L.
A. marginata Gardner
A. monticola Krpov. & Rig.)
A. pintoi Krakov. & W.C. Greg.
A. prostrata Benth.
A. pusilla Benth.
A. stenosperma Krapov & W.C. Greg
A. villosa Benth.
A. villosulicarpa Hoehne

Argyrolobium

A. adscendens Walp.
A. amplexicaule (E. Mey.) Dümmer, as *A. pilosum*
A. biebersteinii P. Ball, as *A. calycinum*
A. candicans Eckl. & Zeyh.
A. collinum Eckl. & Zeyh.
A. eylesii Baker f.
A. filiforme Eckl. & Zeyh.
A. flaccidum (Royle) Aub. & Spach
A. harveyanum Oliv., as *A. uniflorum*
A. humile E. Phillips
A. lanceolatum Eckl. & Zeyh.
A. lancifolium Burtt Davy
A. lunare (L.) Druce Yates et al. pers. comm. (2008)
A. megarrhizum Bolus
A. molle Eckl. & Zey.
A. patens Eck. & Zeyh.
A. pauciflorum Eckl. & Zeyh. and var. *semiglabrum* Harv.
A. pilosum Harv. = *A. amplexicaule*
A. pumilum Eckl. & Zeyh.
A. roseum (Cambess.) Jaub. & Spach subsp. *orthnithopodioides* (Jaub. & Spach.) Jafri & Ali
A. rupestre (E. Mey.) Walp. and subsp. *rupestre* (E. Mey.) Walp.
A. sericeum Eckl. & Zeyh.
A. speciosum Eckl. & Zeyh.
A. stenophyllum Boiss.
A. stipulaceum Eckl. & Zeyh.
A. tomentosum (Andrews) Druce
A. transvaalense Schinz
A. tuberosum Eckl. & Zeyh.
A. uniflorum Harv. = *A. harveyanum*
A. variopile N.E. Br., as *Lotononis magnistipulata* Dümmer
A. zanonii (Turra) P.W. Ball

Aspalathus

A. abietina Thunb.
A. acicularis E. Mey. subsp. *acicularis* E. Mey.
A. acuminata Lam.
A. albens L.
A. alopecurus Benth.
A. angustifolia (Lam.) R. Dahlgren and subsp. *angustifolia* (Lam.) R. Dahlgren
A. araneosa L.
A. argyrophanes R. Dahlgren
A. aspalathoides (L.) R. Dahlgren
A. asparagoides L.f. subsp. *rubro-fusca* (Eckl. & Zeyh.) R. Dahlgren
A. astroites L.
A. biflora E. Mey.
A. bodkinii Bolus Yates et al. pers. comm. (2008)
A. bracteata Thunb.
A. capensis (Walp.) R. Dahlgren
A. carnosa Bergius
A. cephalotes Thunb. subspp. *cephalotes* Thunb. and *violacea* R. Dahlgren
A. cheonpoda L.
A. chortophila Eckl. & Zeyh. subsp. *chortophila* Eckl. & Zeyh.
A. ciliaris L.
A. cinerascens E. Mey.
A. cliffordiodes Bolus
A. commutata (Vogel) R. Dahlgren
A. confusa R. Dahlgren
A. contaminatus Druce
A. cordata (L.) R. Dahlgren
A. crassisepala R. Dahlgren
A. crenata (L.) R. Dahlgren
A. divaricata Thunb. subsp. *divaricata* Thunb.
A. ericifolia L. subspp. *divaricata* Thunb. *ericifolia* L. and *minuta* R. Dahlgren
A. flexuosa Thunb.

A. forbesii Harv.
A. frankenioides DC.
A. gerrardii Bolus
A. hispida Thunb. subspp. *albiflora* (Eckl. & Zeyh.) R. Dahlgren and *hispida* Thunb.
A. hystrix L.f.
A. inops Eckl. & Zeyh.
A. juniperina Thunb.
A. lactea Thunb. subsp. *adelphea* R. Dahlgren = *A. subtingens*
A. laeta Bolus
A. laricifolia Bergius subsp. *canescens* (L.) R. Dahlgren
A. linearis (Burm. f.) R. Dahlgren subsp. *linearis* (Murm.f.) R. Dahlgren
A. linguiloba R. Dahlgren
A. longifolia Benth.
A. longipes Harv.
A. macrantha Harv.
A. microphylla DC.
A. muraltioides Eckl. & Zeyh.
A. neglecta T.M. Salter
A. nigra L.
A. opaca Eckl. & Zeyh. subsp. *opaca* Eckl. & Zeyh.
A. pendula R. Dahlgren Yates et al. pers. comm. (2008)
A. recurva Benth.
A. retroflexa L. subsp. *retroflexa* L.
A. quiquefolia subsp. *virgata* (Thunb.) R. Dahlgren
A. rubens Thunb.
A. salteri L. Bolus
A. sarcodes Vogel & Walp. = *A. capensis*
A. sericea Bergius subsp. *sericea* Bergius
A. setacea Eckl. & Zeyh.
A. spicata Thunb. subspp. *neglecta* (T.M. Salter) R. Dahlgren and *spicata* Thunb.
A. spinescens Thunb. subsp. *lepida* (E. Mey.) R. Dahlgren
A. spinosa L. subsp. *spinosa* L.
A. stenophylla Eckl. & Zeyh. subsp. *garciana* Benth.
A. subtingens Eckl. & Zeyh.
A. teres Eckl. & Zeyh. subsp. *teres* Eckl. & Zeyh.
A. triqueta Thunb.
A. ulicina Eckl. & Zeyh. subsp. *ulicina* Eckl. & Zeyh.
A. uniflora L. subsp. *uniflora* L.

Astragalus

A. adpressus Labill.
A. adsurgens Pall.
A. agrestis Dougl. ex Hook. = *A. danicus* var. *dasyglottis* (*A. alopecuroides* L., may be a synonym for *A. pecurus* Pall.)
A. algerianus E. Sheldon Zakhia et al. (2006)
A. alpinus L. and subsp. *arcticus* Lindman, as *A. subpolaris*
A. americanus (Hook.) M.E. Jones
A. amherstianus Benth. Athar (2005)
A. ammodytes Pall.
A. ammophilus Kar. & Kir. = *A. perepolitanus* Boiss.
A. angustifolius Lam, as *A. leucophyllus*
A. annularis Forssk.
A. arenarius L.
A. aristatus L'Hérit. = *A. sempervirens* subsp. *sempervirens*
A. argophyllus Torr. & A. Gray
A. armatus Willd.
A. asper Jacq.
A. atropilosulus (Hochst.) Bunge subsp. *burkeanus* (Harv.) J.B. Gillett
A. austrinus Small = *A. nuttallianus* var. *austrinus*
A. beckwithii Torr. & A. Gray
A. berytheus Boiss.
A. bisulcatus (Hook.) A. Gray
A. bodinii Sheldon var. *yukonis* (M.E. Jones) Boivin, as *A. yukonis*
A. boeticus L.
A. bolanderi A. Gray
A. brachycarpus M. Bieb.
A. brazoensis Buckley
A. callichrous Boiss.
A. campylosema Boiss.
A. canadensis L.
A. centralpinus Braun-Blanq.
A. ceramicus var. *filifolius* (A. Gray) F.J. Herm.
A. chaborasicus Boiss. & Haussk.
A. chinensis L.f.
A. chrysopteris Bunge Wei et al. (2008)
A. cicer L.
A. chlorostachys Lindl.
A. complanatus Bunge
A. coronilloides Ulbr.
A. corrugatus Bertol., as *A. cruciatus*
A. crassicarpus Nutt. and var. *berlandieri* Barneby
A. coulteri Benth. = *A. lentigenosus* var. *borreganus*
A. cruciatus Link = *A. corrugatus*
A. danicus Retz. var. *dasyglottis* (DC.) Boivin, as *A. agrestis*
A. dahuricus Koch
A. decumbens A. Gray = *A. miser* var. *decumbens*
A. densiflorus Kar. & Kir.
A. drummondii Dougl.
A. dschimensis Gontsch.
A. echinatus Murr.
A. echinus C. Mey.
A. epiglottis Linn
A. eucosmus Robinson = *A. sealei*
A. falcatus Lam.
A. falciformis Desf.
A. flexuosus (Hook.) Dougl.
A. frigidus (L.) Bunge
A. galegiformis L.
A. gambelianus Sheldon
A. glaux Linn

A. glycyphyllos L.
A. gombo Coss. & Dur. ex Bunge
A. gracilis Nutt.
A. gummifer Labill.
A. hamosus L.
A. harringtonii Coville & Standl. = *A. robbinsii* var. *harringtonii*
A. himalayanus Klotzsch
A. hosackioides Benth. ex Baker
A. hornii A. Gray
A. hypogaeus Ledeb.
A. hypoglottis L.
A. karkarensis popov.
A. kentrophyta A. Gray
A. kralikii Battand.
A. lasiophilus Ledeb.
A. lehmannianus Bunge
A. lentiginosus Hook. vars. *borreganus* M.E. Jones, as *A. coulteri* and *fremontii* (A. Gray) S. Watson
A. leontinus Wulfen
A. leptocarpus Torr. & A. Gray
A. leucophyllus Torr. & A. Gray = *A. angustifolius*
A. leucopsis (Torr. & A. Gray) Torr. = *A. trichopodus* var. *lonchus*
A. lindheimeri A. Gray
A. lonchocarpus Torr.
A. lusitanicus Lam. S. Amrani pers. comm. to J.H. Kirkbride (2006)
A. membranaceus Bunge = A. *penduliflorus* Lam.
A. mexicanus DC. = *A. nuttallii*
A. miniatus Bunge
A. miser Hook. var. *decumbens* (Torr. & A. Gray) Cronq., as *A. decumbens*
A. missouriensis Nutt.
A. mollissimus Torr.
A. mongholicus Bunge
A. monspessulanus L.
A. mortoni Nutt.
A. neglectus (Torr. & A. Gray) Sheldon
A. nigrescens Nutt. = *A. tenellus*
A. nuttallianus DC. var. *austrinus* (Small) Barneby, as *A. austrinus*
A. nuttallii (Torr. & A. Gray) J. Howell, as *A. mexicanus*
A. odoratus Lam.
A. orbiculatus Ledeb.
A. oxyglottis Steven ex M. Bieb.
A. pectinatus (Hook.) G. Don
A. pehuenches Niederl., as *A. striatus*
A. pelecinus (L.) Barneby subsp. *pelecinus* (L.) Barneby, = *Biserrula pelecinus* L.
A. podocarpus C. Mey.
A. ponticus Pall.
A. psilocentros Fisch.
A. purshii Hook.
A. reflexistipulatus Miq.
A. robbinsii A. Gray and var. *harringtonii* (Rydb.) Barneby, as *A. harringtonia*
A. roemeri Simonkai
A. saccocalyx Shren ex Fisch.
A. scaberrimus Bunge
A. sealei Lepage = *A. eucosmus*
A. semibilocularis DC.
A. sempervirens Lam. subsp. *sempervirens* Lam., as *A. aristatus*
A. sesameus L. *A. sikkimensis* Bunge
A. siliquosus Boiss.
A. sinicus L.
A. steinbergianus Sumnev.
A. stenocerus C.A. Mey.
A. stipulatis D. Don
A. striatus Reiche = *A. pehuenches*
A. subpolaris Boriss. & Schischk. = *A. alpinus* subsp. *arcticus*
A. subumbellatus Klozsch
A. sulcatus L.
A. tener A. Gray
A. tenellus Pursh., as *A. nigrescens*
A. tribuloides Del.
A. trichocarpus Grah.
A. trichopodus (Torr. & A. Gray) A. Gray var. *lonchus* (M.E. Jones) Barneby, as *A. leucopsis*
A. triphyllus Pursh., as *Orophaca caespitosa* (Nutt.) Britton
A. umbellatus Bunge
A. utahensis (Torr.) Torr. & A. Gray
A. verus Georgi
A. vexiliflexus J. Sheld.
A. whitneyi A. Gray
A. wootoni J. Sheld.
A. yukonis M.E. Jones = *A. bodinii* var. *yukonis*
A. zingeri Korsh.

Ateleia

A. apetala Griseb.
A. gummifera (Bertero ex DC.) D. Dietr.
A. herbert-smithii Pittier
A. glazioviana Baill.
A. ovata Mohlenbr.

Baphia

B. bequaertii De Wild
B. capparidifolia subsp. *polygalacea* Brummitt Diabate et al. (2005)
B. laurifolia Baill.
B. massaiensis subsp. *obovata* (Schinz) Brummitt
B. maxima Baker
B. nitida Lodd
B. pubescens Hook f.

Baptisia

B. alba (L.) Vent., also as *B. leucantha*
B. australis (L.) R. Br.

B. bracteata Elliott and var. *glabrescens* (Larisey) Isely, as *B. leucophaea*
B. lactea (Raf.) Thieret
B. leucantha Torr. & A. Gray = *B. alba* var. *macrophylla* (Larisey) Isely
B. leucophaea Nutt. = *B. bracteata* var. *leucophaea*
B. tinctoria (L.) Vent.

Bergeronia

B. sericea Micheli

Biserrula

B. pelecinus L.

Bituminaria

B. acaulis (Hoffm.) C.H. Stirt., as *Aspalthium acaulis* (Stev.) Kuntze and *Psoralea acaulis* Stev.
B. bituminosa (L.) C.H. Stirt., as *Aspalthium bituminosum* (L.) Kuntze and *Psoralea bituminosa* L.

Bobgunnia

B. madagascariensis (Desv.) J.H. Kirkbr. & Wiersema, as *S. madagascariensis*

Bolusia

B. rhodesiana Corbishley

Bossiaea

B. aquifolium Benth.
B. bossiaeoidea (A. Cunn. ex Benth.) Court
B. buxifolia A. Cunn.
B. cinerea R. Br.
B. dentata Benth.
B. ensata DC.
B. eriocarpa (R. Br.) Benth.
B. foliosa A. Cunn.
B. heterophylla Benth.
B. laidlawiana Tovar & Morrisson
B. linophylla R. Br.
B. ornata (Lindl.) Benth.
B. preissii Meisn.
B. prostrata R. Br.
B. pulchella Meisn.
B. webbii F. Muell.

Bolusafra

B. bituminosa (L.) Kuntze

Bolusanthus

B. speciosus (Bolus) Harms

Bowdichia

B. nitida Benth.
B. virgiloides Kunth

Brongniartia

B. intermedia Moric.

Brya

B. ebenus (L.) DC
B. microphylla Bisse.

Bryaspis

B. lupulina (Planch.) Duvign.

Cadia

C. ellisiana Baker
C. purpurea (Piccivi.) Aiton
C. varia L'Her. Diss. = *C. purpurea*

Cajanus

C. cajan (L.) Millsp.
C. goensis Dalzell
C. lineatus (Wight & Arn.) L.J.G, van der Maesen, as *Atylosia lineata*
C. mollis (Benth.) van der Maesen
C. platycarpus (Benth.) L.J.G. van der Maesen, as *A. platycarpa*
C. scarabaeoides (L.) Thouars, as *A. scarabaeoides* (L.) Benth
C. sericeus (Benth. ex Baker) Maesen.

Calia

C. arizonica (S. Watson) Yakovlev, as *Sophora arizonica*
C. secundiflora (Ortega) Yakovlev, as *S. secundiflora*

Calitome

C. spinosa (L.) Link

Callerya

C. megasperma (F. Muell.) Schott, as *Millettia megasperma*
C. speciosa (Champ.) Schot., as *Millettia speciosa*

Calobota Eckl. & Zeyh.

C. cytisoides (Berg.) Boatwr. & B-E van Wyk, as *Lebeckia cytisoides*
C. linearifolia (E.Mey) Boatwr. & B-E van Wyk, as *L. linearifolius*
C. pungens (Thunb.) Boatwr. & B-E van Wyk, as *L. pungens* Phallane et al. (2008)

C. sericea (Ait.) Boatwr. & B-E van Wyk, as *L. multiflora*
C. spinescens (Harv.) Boatwr. & B-E van Wyk, as *L. spinescens*
C. thunbergii Boatwr. & B-E van Wyk, as *L. sericea*

Calophaca

C. tianshanica (B.Fedtsch.) Suav.

Calopogonium

C. caeruleum (Benth.) Sauvalle
C. mucunoides Desv.
C. orthocarpum Urb. = *C. mucunoides*

Calpurnia

C. aurea (Aiton) Benth.
C. intrusa (Aiton f.) E. Mey. = *C. villosa*
C. villosa Harv.

Camptosema

C. coriaceum (Ness & Mart.) Benth.
C. pedicellatum Benth.
C. rubicundum Hook & Arn.

Campylotropis

C. macrocarpa (Bunge) Rehder
C. meeboldii (Schindl.) Schindl.

Canavalia

C. africana Dunn
C. brasilensis Mart. ex Benth.
C. campylocarpa Piper
C. cathartica Thouars
C. ensiformis (L.) DC.
C. gladiata (Jacq.) DC. and var. *gladiata* (Jacq.) DC.
C. lineata (Thunb.) DC.
C. maritima (Aublet) Thouars, = *C. rosea*
C. rosea (Sw.) DC., as *C. maritima*
C. virosa (Roxb.) Wight & Arn. = *C. cathartica*

Caragana

C. ambigua Stocks
C. arborescens Lam.
C. aurantiaca Koehne
C. brevispina Benth.
C. decorticans Hemsl.
C. erinacea Kom.
C. frutescens (L.) Medik. = *C. frutex*
C. frutex (L.) K. Koch
C. intermedia Kuang & H.C. Fu = *C. korshinskii*
C. korshinskii Kom.
C. leveillei Kom.
C. maximowicziana Kom. = *C. erinacea*
C. microphylla Lam.
C. pekinensis Kom. = *C. zalbruckneri* var. *pekinesis*
C. pleiophylla (Regel) Pojark.
C. polourensis Franch.
C. pruinosa Korn.
C. rosea Turcz. ex Maxim.
C. sinica (Buc'hoz) Rehder
C. sophoraelia x Tausch
C. tragacanthoides Poir.
C. turkestanica Kom.
C. versicolor Benth.
C. zalbruckneri var. *pekinesis* (Kom.) Yakovlev

Carmichaelia

C. aligera Simpson = *C. australis*
C. angustata Kirk = *C. odorata*
C. arborea (Forst. f.) Druce
C. arenaria Simpson) = *C. australis*
C. australis R. Br.
C. crassicaule Hook.f., as *Corallospartium crassicaule* (Hook.f.) Armstr.
C. exsul F. Muell.
C. flagelliformis Hook.f. = *C. australis*
C. glabrescens (Petrie) Heenan, as *Notospartium glabrescens* Petrie
C. grandiflora Hook.f. = *C. arborea*
C. kirkii Hook.f.
C. monroi Hook.f.
C. nana Hook.f.
C. odorata Hook.f.
C. orbiculata Hook.f. = *C. nana*
C. ovata Simpson = *C. australis*
C. petriei Kirk
C. robusta Kirk = *C. australis*
C. stevensonii (Cheeseman) Heenan, as *Chordospartium stevensonii* Cheeseman
C. subulata Kirk
C. violacea Kirk = *C. australis*
C. virgata Kirk = *C. petrei*
C. williamsii Kirk

Centrolobium

C. parense Tul.
C. robustum (Vell.) Benth.
C. tomentosum Benth.

Centrosema

C. acutifolium Benth.
C. angustifolium (Kunth) Benth.
C. arenarium Benth.
C. brasilianum (L.) Benth.
C. macrocarpum Benth.)
C. molle Benth. = *C. pubescens*
C. pascuorum Benth.
C. plumieri (Pers.) Benth.
C. pubescens Benth.
C. rotundifolium Mart. ex Benth.
C. sagittatum (Humb. & Bonpl. ex Willd.) Brandegee

C. schottii (Millsp.) K. Schum.
C. venosum Benth.
C. vexillatum Benth. S.M. de Faria pers. comm. to J.H. Kirkbride (2006)
C. virginianum (L.) Benth. and var. *latifolium* (L.) Benth.

Chadsia

Chadsia grevei Drake.

Chapmannia

C. prismatica (Sessé & Moçinõ) Standl. & B.G. Schub.

Chesnya

C. ternata (Korsh.) Popov

Chorizema

C. aciculare (DC.) C. Gardner
C. cordatum Lindl.
C. cytisoides Turcz.
C. dicksonii Graham
C. diversifolium A. DC.
C. ericifolium Meisn.
C. ilicifolium Labill.
C. parviflorum Benth.
C. reticulatum Meisn.

Christia

C. obcordata (Poir.) Bakh.f.
C. vespertilionis (L.f.) Bakh.f.

Cicer

C. arietinum L.
C. chorassanicum Popov
C. pinnatifidum Jaub. & Spach

Clathrotropis

C. brachypetala (Tul.) Kleinhoonte
C. macrocarpa Ducke
C. nitida (Benth.) Harms

Cleobullia

C. multiflora Mart. ex Benth.

Clianthus

C. formosus (G. Don) Ford & Vick. = *Swainsona formosa*
C. puniceus (G. Don) Lindl.

Clitoria

C. amazonum Mart. ex Benth.
C. annua J. Graham, as *C. biflora*
C. arborea Benth. S.M. de Faria pers. comm. to J.H. Kirkbride (2006)
C. australis Benth.
C. biflora Dalz. = *C. annua*
C. fairchildiana Howard
C. falcata Lam.
C. guianensis (Aubl.) Benth.
C. javitensis (Kunth) Benth.
C. laurifolia Poir.
C. mariana L.
C. rubiginosa Pers. = *C. falcata*
C. sagotii Fantz.
C. ternatea L.

Codariocalyx

C. gyrans (L.f.) Hassk. = *C. motorius*
C. gyroides (Link) Hassk., as *Desmodium gyroides*
C. motorius (Houtt.) H. Ohashi, as *Desmodium gyrans.*

Collaea

C. speciosa (Loisel) DC. Lemmel et al. (2007)

Cologania

C. angustifolia Kunth
C. broussonetti DC.

Colutea

C. arborescens L.
C. istria Mill.
C. silicica Boiss. & Bal.
C. nepalensis Sims
C. orientalis Mill.
C. persica Boiss.

Corethrodendron

C. fruticosum (Pall.) B.H.Choi & H. Ohashi, as *Hedysarum fruticosum*
C. scoparium (Fisch. & C.A.Mey.) Fisch. ex Basiner, as *H. scoparium*

Coronilla

C. cappadocica Willd. = *Securigera orientalis*
C. coronata L.
C. cretica L. = *Securigera cretica*
C. emerus L. = *Hippocrepis emerus* subsp. *emerus*
C. glauca L. = *C. valentina* subsp. *glauca*
C. montana Scop. = *C. coronata*
C. pentaphylla Desf. = *C. valentina* subsp. *pentaphylla*
C. repanda (Poir.) Guss.
C. scorpioides (L.) Koch
C. vaginalis Lam., as *Arthrolobium vaginalis* (Lam.) Desv.
C. valentina L. and subspp. *glauca* (L.) Batt., and *pentaphylla* (Desf.) Batt.
C. varia L. = *Securigera varia*

Coursetia

C. arborea Griseb. = *C. ferruginea*
C. caribaea (Jacq.) Lavin, as *Cracca caribaea* (Jacq.) Oersted
C. cathartica, as *Cracca cathartica* Rydb. = *Tephrosia senna* Kunth
C. ferruginea (Kunth) Lavin, as *C. arborea*

Craibia

C. brevicaudata (Vatke) Dunn

Cranocarpus

C. martii Benth.

Cratylia

C. argentea (Desv.) Kuntze, as *C. floribunda*
C. hypargyraea Benth.
C. floribunda Benth. = *C. argentea*

Crotalaria

C. abbreviata Baker f.
C. acicularis Benth.
C. agatifolia Schweinf.
C. alata D. Don)
C. albida Roth
C. alexandri Baker f.
C. allenii Verd. = *C, orientalis* subsp *allenii* Polhill & A. Schreib.
C. anagyroides Kunth = *C. micans*
C. angulata Mill.
C. anisophylla (Hiern) Baker
C. anthyllopsis Baker
C. argyrea Welw.
C. assamica Benth.
C. astragalina Hochst. = *C. impressa* Nees ex Walp
C. atrorubens Hochdt. ex Benth.
C. axillaris Aiton
C. australis Baker f. = *C. laburnifolia* subsp. *australis*
C. barkae Schweinf.
C. barnabassii Baker f.
C. bequaertii Baker f.
C. berteroana DC.
C. brachycarpa (Benth.) Verd.
C. bracteata = *C. nitens*
C. brevidens Benth.
C. breviflora DC. var. *pobliana* (Benth.) Windler & Skinner, as *C. ferruginea* Scheele
C. brownei DC.
C. burhia Buch.-Ham.
C. burkeana Benth.
C. cajanifolia Kunth
C. calycina Schrank
C. capensis Jacq.
C. caudata Baker
C cephalotes A. Rich.
C. chinensis Roxb.(?)
C. chirindae Baker f.
C. cleomifolia Baker
C. collina Polhill
C. comosa Baker
C. cunninghamii R. Br.
C. cylindrocarpa DC. Diabate et al. (2005)
C. cylindrostachys Baker
C. cytisoides Roxb. ex DC.
C. damarensis Engl.
C. deserticola Baker f.
C. dissitiflora Benth.
C. distans Benth. and subspp. *macaulayae* (Baker f.) Polhill and *macrotropis* (Baker f.) Polhill
C. doidgeae Verd.
C. doniana Baker
C. dura J.M. Wood & Evans
C. erecta Pilg.
C. eremaea F. Muell. subsp *eremaea*
C. eremicola Baker f.
C. eriocarpa Benth. = *C. cajanifolia*
C. falcata Vahl ex DC. = *C. pallida*
C. ferruginea Scheele = *C. breviflora* var. *pobliana*
C. filicaulis Baker
C. filipes Benth.
C. flavicarinata Baker f.
C. fulva Roxb. = *C. berteroana*
C. gazensis Baker f. subsp. *gazensis* Baker f.
C. glauca Willd.
C. glaucoides Baker f.
C. globifera E. Mey.
C. goreensis Guill. & Perr.
C. grantiana Harv. = *C. virgulata* subsp. *grantiana* (Harv.) Polhill
C. hainanensis Huang
C. hebecarpa (DC.) V.E. Rudd as *Heylandia latebrosa* DC.
C. heidimannii Schinz
C. hildebrantii Vatke = *C. axillaris*
C. hispida Schinz = *C. steudneri*
C. holosericea Nees & Mart.
C. humifusa Benth.
C. humilis Eckl. & Zeyh.
C. hyssopifolia Klotzsch
C. incana L. and subsp. *purpurascens* (Lam.) Milne-Redh.
C. insignis Polhill
C. intermedia Kotschy = *C. brevidens* var *inermedia* (Kotschy) Polhill
C. juncea L.
C. kapirensis De Wild.
C. kipandensis Baker f.
C. laburnifolia L. subspp. *australis* (Baker f.) Polhill and *laburnifolia* L.
C. lachnocarpoides Engl.
C. lachnophora A. Rich.
C. lachnosema Stapf Diabate et al. (2005)
C. lanceolata E. Mey. and subspp. *lanceolata* E. Mey. and *prognatha* Polhill
C. lasiocarpa Polhill
C. lathyroides Guill. & Perr.

C. leptostachya Benth.
C. linifolia L.f.
C. longirostrata Hook. & Arn.
C. longithyrsa Baker f.
C. lotoides Benth.
C. lupulina Kunth = *C. pumila*
C. macrocarpa E. Mey.
C. macaulayae Baker f. = *C. distans* subsp. *macaulayae*
C. maypuensis Kunth
C. medicaginea Lam.
C. meyerana Steud.
C. micans Link
C. microcarpa Benth.
C. mitchellii Benth.
C. mucronata Desv. = *C. pallida*
C. mundyi Baker = *C. distans* subsp *macrotropis* (Baker f.) Polhill
C. mysorensis Roth
C. nana Burm.f.
C. natalitia Meisn. and vars. *natalitia* Meisn. and *rutshuruensis* De Wild.
C. nitens Kunth
C. obscura DC.
C. ochroleuca G. Don
C. oocarpa Baker
C. orixensis Willd.
C. orthocalada Welw.
C. pallida Aiton and var. *pallida* Aiton
C. pallidicaulis Harms
C. paulina Schrank
C. perrottii DC.
C. phylicoides Wild
C. pilosa Mill.
C. pisicarpa Baker
C. platysepala Harv.
C. podocarpa DC.
C. polysperma Kotschy
C. prostrata Rottler ex Willd.
C. pseudo-eriosema Vatke = *C. vasculosa*
C. pumila Ortega
C. quinquefolia L.
C. recta A. Rich.
C. reptans Taub.
C. retusa L.
C. rhodesiae Baker f.
C. rogersii Baker f.
C. rotundifolia J. Gmel.
C. sagittalis L.
C. saharae Coss.
C. saltiana Andrews
C. schinzii Baker f.
C. schlechteri Baker f.
C. semperflorens Vent. = *C. verrucosa*
C. senegalensis (Pers.) DC.
C. sessiliflora L.
C. shirensis (Baker f.) Milne-Redh.
C. sparsifolia Baker
C. spartea Baker
C. spectabilis Roth
C. sphaerocarpa DC.
C. spinosa Benth.
C. steudneri Schweinf.
C. stipularia Desv.
C. stolzii (Baker f.) Polhill var. *stolzii* (Baker f.) Polhill
C. striata DC. = *C. pallida*
C. stricta Roxb.
C. subcapitata De Wild. subsp. *subcapitata* De Wild.
C. tetragona Andrews
C. trichotoma Boger
C. trifoliastrum Willd.
C. triquetra Dalzell
C. usaramoensis Baker f. = *C. trichotoma*
C. valetonii Backer
C. valida Baker
C. vallicola Baker f.
C. variegata Baker
C. vasculosa Benth.
C. velutina Benth.
C. verrucosa L.
C vestita Baker
C. virgulata Klotzsch and subsp. *grantiana* (Harv.) Polhill
C. zanzibarica Benth.

Cullen

C. americanum (L.) Rydb.
C. australasicum Dear et al. (2007)
C. cinereum, (Lindl.) J.W.Grimes, as *Psoralea cinerea*
C. corylifolium (L.) Medik. as *P. coryfolia*
C. lachnostachys (F. Muell.) J.W.Grimes
C. martini (F. Muell.) J.W. Grimes
C. microcephalum (Rchb. ex Kunze) J.W. Grimes
C. obtusifolium (DC.) C.H. Stirt. = *C. tomentosum*.
C. parvum Dear et al. (2007)
C. patens (Lindl.) J.W.Grimes, as *P. patens*
C. tenax (Lindl.) J.W.Grimes, as *P. tenax*
C. tomentosum (Thunb.) J.W. Grimes

Cyamopsis

C. dentata (N.E.Br.) Torre
C. serrata Schinz
C. tetragonoloba (L.) Taub.

Cyathostegia

C. mathewsii (Benth.) Schery.

Cyclocarpa

C. stellaris Baker

Cyclolobium

C. vecchii Hoehne

Cyclopia

C. falcata (Harv.) Kies
C. galioides (Bergius) DC. Elliott et al. (2007b)
C. genistoides var *genistoides* (L.) R. Br.
C. glabra (Hofmeyr & Phillips) A.L. Schutte

C. intermedia E. Mey Elliott et al. (2007b)
C. latifolia DC.
C. longifolia Vogel
C. maculata (Andrews) Kies
C. meyeriana Walp.
C. montana Hofmeyer & E. Phillips = *C. glabra*
C. pubescens Eckl. & Zeyh. Elliott et al. (2007b)
C. sessiliflora Eckl. & Zeyh.
C. subternata Vogel

Cytisophyllum

C. sessilifolium (L.) O. Lang, as *Cytisus sessilifolius* L.

Cytisus

C. austriacus L.
C. borysthenicus Gruner
C. capitatus Jaqc. = *C. hirsutus*
C. decumbens (Durande) Spach
C. fragrans Lam. = *C. supranubius*
C. hillebrandtii Briq. = *Genista hillebrandtii*
C. hirsutus L.
C. multiflorus (L'Her.) Sweet
C. nigricans L. = *Lembotropis nigricans*
C. proliferus L.f. and var. *palmensis* Christ
C. purgans (L.) Boiss.
C. purpureus (Scop.) Link
C. ruthenicus (Wolosz.) Klásk.
C. sagittalis (L.) K. Koch = *Genista sagittalis*
C. scoparius (L.) Link = *Sarothamnus scoparius* (L.) Koch and var. *andreanus* Hort.
C. sessilifolius L. = *Cytisophyllum sessilifolium*
C. supranubius (L.f.) Kuntze, as *C. fragrans*
C. supinus (L.) Link = *C. hirsutus*
C. villosus Pourr.
C. virescens Wohlf.

Dahlstedtia

Dahlstedtia pinnata (Benth.) Malme

Dalbergia

D. albiflora A. Chev. ex Hutch. & Dalziel
D. arbutifolia Baker
D. armata E. Mey.
D. balansae Prain
D. baronii Baker Rasolomampianina et al. (2005)
D. bignonae Berhaut Diabate et al. (2005)
D. boehmii Taub.
D. brasilense Vogel
D. candenatensis (Dennst.) Prain
D. chapeliari Baill. Rasolomampianina et al. (2005)
D. cultrata R.A. Graham
D. decipularis Rizz. & Mattos
D. ecastaphyllum (L.) Taub.
D. fischeri Taub.
D. frutescens (Vell. Conc.) Britton
D. glaucescens (Benth.) Benth.
D. hancei Benth.
D. hainanensis
D. horrida (Dennst.) Mabb.
D. hortensis Heringer Rizzini & A. Mattos
D. hostilis Benth.
D. hupeana Hance
D. inundata Benth.
D. lactea Vatke
D. lanceolaria L.f.
D. latifolia Roxb.
D. louvelii R. Vig. Rasolomampianina et al. (2005)
D. madagascariensis Vatke Rasolomampianina et al. (2005)
D. maritima Rasolomampianina et al. (2005)
D. martinii F. White
D. melanoxylon Guill. & Perr.
D. millettii Benth. Ng & Hau (2009)
D. miscolobium Benth.
D. monetaria L.f.
D. monticola Bosser & R. Rabev Rasolomampianina et al. (2005)
D. nigra (Vell.) Allemão ex Benth.
D. nitidula Baker
D. obovata E. Mey.
D. obtusifolia Prain
D. odorifera T.C. Chen)
D. oligophylla Hutch. & Dalziel
D. paniculata Roxb. = *D. lanceolaria* sub sp *paniculata* (Roxb.) Thoth.
D. pinnata Prain =*Derris pinnata*
D. purpurascens Baill. Rasolomampianina et al. (2005)
D. retusa Hemsl.
D. riedelii (Radlk.) Sandwith
D. riparia (Mart.) Benth.
D. sissoo Roxb.
D. spruceana Benth.
D. stipulacea Roxb.
D. sympathetica Nimmo = *D. horrida*
D. szemaoensis Prain = *D, lanceolaria* sub sp *assamica* (Benth.) Thoth.
D. trichocarpa Baker Rasolomampianina et al. (2005)
D. tsoi Merr. & Chun
D. villosa (Benth.) Benth.

Dalbergiella

D. nyasae Baker f.

Dalea

D. albiflora A. Gray, as *D. ordiae* Gray
D. alopecuroides Willd. = *D. leporina*
D. aurea Fraser
D. candida Willd., as *Petalostemon candida* (Willd.) Michx. and var. *oligophylla* (Torr.) Shinners, as *P. oligophyllus* (Torr.) Rydb.
D. cliffortiana Willd.
D. erythrorhiza Greenm. James et al. (2007) unpub
D. frutescens A. Gray
D. lagopus (Cav.) Willd. = *D. leporina*
D. leporina (Aiton) Bullock
D. lumholtzii Robinson & Fern.
D. multiflora (Nutt.) Shinn., as *P. multiflorus* Nutt.
D. mollissima (Rydb.) Munz
D. parryi Torr. & A. Gray = *Marina parryi*
D. phleoides (Torr. & A. Gray) Shinn. var. *microphylla* (Torr. & A. Gray) Barneby, as *P. microphyllum* (Torr. & A. Gray) A. Heller
D. pogonathera A. Gray
D. purpurea Vent., as *P. purpureum* (Vent.) Rydb.
D. spinosa (A. Gray) = *Psorothamnus spinosus*
D. tenuis (Coult.) Shinn., as *P. stanfieldii* Small
D. villosa (Nutt.) Spreng., as *P. villosus* Nutt.
D. virgata Lag.

Daviesia

D. acicularis Sm.
D. aphylla (F. Muell.) Benth. = *D. benthamii* sub sp *acanthoclona*
D. benthamii sub sp. *acanthoclona* (F. Muell.) Crisp
D. brevifolia Lindl.
D. buxifolia Benth.
D. cordata Sm.
D. corymbosa Sm.
D. decurrens Meisn.
D. flexuosa Benth.
D. genistifolia Cunn.
D. hakeoides Meisn.
D. horrida Meisn.
D. incrassata Sm.
D. latifolia R. Br.)
D. leptophylla A. Cunn. ex G. Don
D. mimosoides R. Br.
D. nudiflora Meissner A. McInnes pers. comm. (2007)
D. pectinata Lindl.
D. reversifolia F. Muell. = *D. incrassata* sub sp. *reversifolia* (F. Muell.) Crisp
D. teretifolia R. Br.
D. ulicifolia Andrews
D. umbellulata Sm.

Decorsia

D. schlechteri (Harms) Verdc.

Deguelia

D. amazonica Killip
D. costata (Benth.) A.M.G. Azevedo
D. negrensis (Benth.) Taub.
D. scandens Aublet, *as Derris negrensis* and *D. longifolia*
D. spruceana (Benth.) Ducke, as *Lonchocarpus spruceanus* Benth.

Dendrolobium

D. dispermum Schindl.
D. triangulare (Retz.) Schindl., as *Desmodium triangulare* (Retz.) Merr.
D. umbellatum (L.) Benth.

Derris

D. amazonica Killip = *Lonchocarpus negrensis*
D. elliptica (Roxb.) Benth. = *Pongamia pinnata*
D. latifolia (Kunth) Ducke = *Lonchocarpus discolor*
D. longifolia Benth. = *Deguelia scandens*
D. microphylla (Miq.) Backer
D. negrensis Benth. = *Deguelia scandens*
D. philippinensis Merr.
D. robusta (DC.) Benth.
D. scandens (Roxb.) Benth. = *Deguela scandens*

Desmodium

D. adscendens (Sw.) DC. and var. *robustum* Schub.
D. affine Schltdl.
D. asperum Desv.
D. auriculatum DC. = *Tadehagi triquetrum* subsp. *auriculatum* (DC.) H. Ohashi
D. axillare (Sw.) DC. vars. *acutifolium* (Kuntze) Urb., as *Nephromeria axillaris* var. *acutifolioloa* (Urb.) Schindl. and *genuinum* Urb.
D. barbatum (L.) Benth.
D. batocaulon A. Gray
D. biarticulatum F. Muell. = *Aphyllodium biarticulum* (L.) Gagnep.
D. blandum Meewen =*Phyllodium elegans*
D. bracteosum (Michx.) DC. = *D. cuspidatum*
D. cajanifolium (Kunth) DC.
D. campylocaulon Benth.
D. canadense (L.) DC.

D. canescens (L.) DC.
D. canum (J.F. Gmel.) Schinz & Thell. = *D. incanum*
D. capitatum DC. = *D. styracifolium*
D. caudatum (Thunb.) DC., now *Ohwia caudata*
D. ciliare (Willd.) DC. = *Codariocalyx gyroides* (Roxb. ex Link) Hassk.
D. cinereum DC.
D. concinnum DC.
D. confertum DC.
D. cuneatum Hook. & Arn.
D. cuspidatum (Willd.) Loudon
D. dichotomum (Willd.) DC.
D. diffusum (Roxb.) DC. = *D. laxiflorum*
D. dillenii Darl.
D. discolor Vogel
D. distortum (Aubl.) J.F. Macbr.
D. dregeanum Benth.
D. elegans Benth. = *Phyllodium elegans* (Lour.) Desv.
D. fallax Schindl. and subsp. *mandshuricum* (Maxim.) Nakai = *D. podocarpum* subsp. *fallax* (Schindl.) H. Ohashi
D. filiforme Hook.f. = *D. limense*
D. flagellare Benth.
D. floribundum (D. Don) Sweet = *D. multiflorum* DC.
D. gangetum (L.) DC.
D. glabrum (Mill.) DC., as *D. molle*
D. glutinosum (Willd.) Alph. Wood, now *Hylodesmum glutinosum*
D. gyrans DC = *Codariocalyx motorius*
D. gyroides (Link) DC. = *Codariocalyx gyroides*
D. heterocarpon (L.) DC.
D. heterophyllum (Willd.) DC.
D. hirtum Guill. & Perr.
D. hookerianum D. Dietr.
D. illinoense A. Gray
D. incanum DC., as *D. canum*
D. intortum (Mill.) Urb.
D. jucundum Thwaites
D. laevigatum (Nutt.) DC.
D. latifolium DC. = *D. velutinum*
D. laxiflorum DC.
D. leiocarpum (Spreng.) G. Don
D. limense Hook.
D. limenses var. *sandwicense* Schinde = *D. sandwicense*
D. macrocarpum Domin.
D. marilandicum Darl.
D. microphyllum DC.
D. molliculum (Kunth) DC.
D. muelleri Benth.
D. multiflorum DC.
D. natalitium Sond.
D. nemorosum Benth.
D. nicaraguensis Benth.
D. nudiflorum (L.) DC.
D. oldhami Oliv.
D. oojeinense (Roxb.) H. Ohashi, as *Ougeinia oojeinensis* (Roxb.) Hochr. Roshetko et al. (1996) Now returned to Ougeinia and listed for this genus, but as sp *O. dalbergioides*,
D. ospriostreblum Chiov.
D. ovalifolium Merr. = *D. heterocarpon* subsp. *ovalifolium* (Prain) H. Ohashi
D. pabulare Hoehne
D. pachyrhizum (Sw.) Vogel
D. paniculatum (L.) DC.
D. pauciflorum (Nutt.) DC., now *Hylodesmum pauciflorum*
D. podocarpum DC. = *P. hookerianum*, now *Hylodesmum podocarpum*
D. procumbens (Mill.) A. Hitchc.
D. pulchellum (L.) Benth. = *Phyllodium pulchellum* (L.) Desv.
D. purpureum (Mill.) Fawcett & Rendle = *D. tortuosum*.
D. racemosum DC. = *D. podocarpum* subsp. *oxyphyllum* (DC.) H. Ohashi
D. repandum (Vahl) DC., now *Hylodesmum repandum*
D. renifolium (L.) Schindl.
D. retinens Schltdl.
D. rhytidophyllum F. Muell.
D. rotundifolium (Michx.) DC.
D. rubrum (Lour.) DC.
D. salicifolium (Poir.) DC. var. *salicifolium* (Poir.) DC.
D. sandwicense E. Mey.
D. scorpiurus (Sw.) Desv.
D. sequax Wall.
D. sessilifolium (Torr. & A. Gray)
D. setigerum (E.Mey.) Harv.
D. sintenisii Urb.
D. sinuatum Blume ex Baker = *D. sequax*
D. styracifolium (Osbeck) Merr.
D. tanganyikense Baker
D. tiliaefolium G. Don = *D. elegans*
D. tortuosum (Sw.) DC.
D. triangulare (Retz.) Merr. = *Dendrolobium triangulare*
D. trichocaulon DC.
D. triflorum (L.) DC.
D. triquetrum (L.) DC. = *Tadehagi triquetrum*
D. umbellatum (L.) DC. = *Dendrobium umbellatum* (L.) Benth.
D. uncinatum (Jacq.) DC.
D. varians (Labill.) G. Don
D. velutinum (Willd.) DC.
D. viridiflorum DC.
D. virgatum Zoll.
D. zonatum Miq.

Dewevrea

D. bilabiata Micheli

Dichilus

D. lebeckoides DC.

D. pilosus Schinz
D. strictus E. Mey.

Dillwynia

D. brunioides Meisn.
D. cinerascens R. Br.
D. divaricata (Turcz.) Benth.
D. ericifolia Sm. = *D. retorta*
D. floribunda Sm.
D. glaberrima Labill.
D. hispida Lindl.
D. juniperina Siebert
D. peduncularis Benth.
D. ramosissima Benth.
D. retorta (Wendl.) Druce, as *D. ericifolia*
D. sericea A. Cunn.
D. uncinata (Turcz.) C. Gardner

Dioclea

D. bicolor Benth.
D. glabra Mart. ex Benth.
D. glycinoides Hort. = *Camptosema rubicundun*
D. guianensis Benth.
D. macrocarpa Huber
D. malacocarpa Ducke
D. reflexa Hook. f.
D. sericea Kunth
D. violacea Benth.
D. virgata (L. Rich.) Amshoff

Diphysa

D. robinoides Benth. ex Benth. & Oerst.

Diplotropis

D. brasiliensis (Tul.) Benth.)
D. incexis Rizz. & A. Mattos
D. purpurea (Rich.) Amshoff var. *purpurea* (Rich.) Amshoff
D. triloba Gleason S.M. de Faria pers. comm. to J.H. Kirkbride (2006)

Dipogon

D. lignosus (L.) Verdc.

Discolobium

D. pulchellum Benth.
D. leptophyllum Benth.
D. psoraliaefolium Benth.

Dolicopsis

D. paraguariensis Hassl.

Dolichos

D. angustifolius Eckl. & Zeyh.
D. debilis Hochst.
D. falciformis E. Mey.
D. hastiformis E. Mey.
D. junghuhnianus Benth.
D. kilimandscharicus Taub.
D. linearis E. Mey.
D. melanophthalmus DC. = *Vigna unguiculata* (L.) Walp.
D. nimbaensis Schnell Diabate et al. (2005)
D. oliveri Schweinf.
D. sericeus E. Mey. subspp. *formosus* (A. Rich.) Verdc. and *sericeus* E. Mey.
D. sesquipedalis L. = *Vigna unguiculata* subsp. *sesquipedalis*
D. tonkouiensis Portères
D. trilobus L. and subspp. *transvaalicus* Verdc. and *trilobus* L.
D. trinervatus Baker

Dorycnium

D. herbaceum Villars = *D. pentaphyllum* subsp. *herbaceum* (Villars) Rouy
D. hirsutum (L.) Ser.
D. pentaphyllum Scop. and subsp. *herbaceum*, as *D. herbaceum*
D. rectum (L.) Ser.
D. spectabile (Choisy ex Ser.) Webb & Berthel
D. suffruticosum Villars. = *D. pentaphyllum*

Droogsmansia

D. pteropus (Baker) De Wild
D. scaettaiana A. Chev. & Sillans Diabate et al. (2005)

Dumasia

D. truncata Siebold & Zucc.
D. villosa DC.

Dunbaria

D. circinalis (Benth.) Baker
D. heynei Wight & Arn.
D. nivea Miq.
D. villosa Makino

Dussia

D. marticensis Krug & Urb.

Dysolobium

D. apioides (Gagnepain) Maréchal

Ebenus

E. pinnata Aiton

Eisenhardtia

X. stuhlmannii (Taub.) Mendonca & Sousa

Eminia

E. antennulifera (Baker) Taub.

Eremosparton

E. songorium (Litv.) Vassilcz.

Eriosema

E. affine De Wild.
E. buchananii Baker f.
E. burkei Harv.
E. chrysadenium Taub.
E. cordatum E. Mey.
E. crinitum (Kunth) G. Don
E. ellipticum Baker
E. englerianum Harms
E. glomeratum (Guill. & Perr.) Hook. f.
E. heterophyllum Benth.
E. junionianum Stauer & De Craene
E. kraussianum Meisn.
E. lebrunii Staner & Craene
E. macrostipulum Baker f.
E. montanum Baker f.
E. nutans Schinz, as E. polystachyum
E. parviflorum E. Mey. and subsp. *collinum* Hepper (the latter Diabate et al., 2005)
E. pauciflorum Klotzsch
E. polystachyum (A. Rich.) Baker, = *E. junionianum*
E. psoraleoides (Lam.) G. Don
E. pumilum Verdc.
E. ramosum Baker f.
E. rhodesicum R.E.Fr.
E. rhynchosioides Baker
E. rufum (Kunth) G. Don
E. salignum E. Mey.
E. shirense Baker f.
E. simplicifolium (Kunth) G. Don
E. squarrosum (Thunb.) Walp.
E. villosum (Meisn.) Burtt Davy = *Rhynchosia villosa*
E. violaceum (Aubl.) G. Don

Erophaca

E. baetica (L.) Boiss. subsp. *baetica* (L.) Boiss, as *Astragalus lusitanicus*

Erythrina

E. america Mill.
E. abyssinica DC.
E. arborescens Roxb.
E. barqueroana Krukoff & Barneby
E. berteroana Urb.
E. bogatensis Hort. = *E. vespertilio*
E. brucei Schweinf. *E. caffra* Thunb.
E. caffra Thunb.
E. corallodendron L.
E. costaricensis M. Micheli
E. crista-galli L.
E. edulis Triana
E. excelsa Baker
E. falcata Benth.
E. folkersii Krukoff & Mold.
E. fusca Lour.
E. glauca Willd. = *E. fusca*
E. herbacea L.
E. hondurensis Standl.
E. horrida DC.
E. humeana Spreng.
E. insignis Tod.
E. lanata Rose Altomarino-Hernandez et al. (2004)
E. lanceolata Standl.
E. latissima E. Mey.
E. livingstoniana Baker
E. lysistemon Hutch.
E. milbraedii Harms Diabate et al. (2005)
E. mitis Jacq., as *E. umbrosa*
E. monosperma Gaudich = *E. tahitensis*
E. pallida Britton
E. poeppigiana (Walp.) O.F.Cook
E. reticulata C. Presl. = *E. speciosa*
E. ribrinervia Kunth
E. sandwicensis O Deg.
E. senegalensis DC.
E. speciosa Andrews, as *E. reticulata*
E. stricta Roxb.
E. suberosa Roxb. = *E. stricta* var *suberosa* (Roxb.) Niyomdham
E. subumbrans (Hassk.) Merr.
E. tahitensis Nadak
E. umbrosa Kunth = *E. mitis*
E. variegata L.
E. velutina Willd.
E. verna Vell.
E. vespertilio Benth.
E. zeyheri Harv.

Etabalia

E. dubia Rudd

Euchilopsis

E. linearis (Benth.) F. Muell.

Euchresta

E. japonica Benth.

Eutaxia

E. densifolia Turcz.
E. epacridioides Meisn.
E. microphylla (R. Br.) J. Black
E. obovata (Labill.) C. Gardner
E. virgata Benth.

Flemingia

F. congesta Roxb. = *F. macrophylla*

F. fruticulosa Wall. = *F. strobilifera*
F. grahamiana Wight & Arn.
F. lineata (L.) Aiton
F. macrophylla (Willd.) Merr., as *F. congesta*
F. philippinensis Merr. & Rolfe
F. procumbens Domin
F. prostrata Roxb.
F. semialata Roxb.
F. strobilifera (L.) Aiton f.

Galactia

G. canescens F.J.Herm
G. crassifolia (Benth.) Taub. Lammel et al. (2007)
G. dubia DC.
G. falcata Benth.
G. jussiaeana Kunth
G. neesii DC., as *Clitoria rubiginosa*
G. regularis (L.) Britton et al.
G. rubra (Jacq.) Urb.
G. striata (Jacq.) Urb.
G. tenuiflora (Willd.) Wight & Arn.
G. volubilis (L.) Britton = *G. regularis*

Galega

G. albiflora Tournay
G. bicolor Boiss. = *G. officinalis*
G. officinalis L.
G. orientalis Lam.
G. patula Stev. = *G. officinalis*

Gastrolobium

G, bilobum R. Br.
G. brownii Meisn.
G. capitatum (Benth.) G.T. Chandler & Crisp
G. celsianum (Lem.) G.T. Chandler & Crisp
G. crassifolium Benth.
G. laytonii J. R. White
G. obovatum Benth.
G. nervosum (Meisn.)
G. parviflorum (Benth.) Crisp, as *Oxylobium parviflorum*
G. pulchellum Turcz.
G. spinosum Benth.
G. trilobum Benth.
G. velutinum Lindl.
G. villosum Benth. from *Brachysema*
B. aphyllum Hook.
B. chambersii (F. Muell.) Benth. = *Leptosema chambersii*
B. lanceolatum Meisn.
B. latifolium R. Br.
B. praemorsum Meisn.
B. sericeum (Smith) Domin from *Nemcia*
N. atropurpurea (Turcz.) Domin
N. capitata (Benth.) Domin
N. leakeana (Drumm.) Crisp, as *Oxylobium atropurpureum*
N. reticulata (Meisn.) Domin

Geissaspis

G. cristata Wight & Arn.
G. tenella Benth.

Genista

G. anglica L.
G. canariensis L., as *Teline canariensis* (L.) Webb & Berth.
G. cinerea (Vill.) DC.
G. ferox Poir.
G. florida L.
G. germanica L.
G. hillebrandtii Christ = *G. canariensis*
G. hispanica L.
G. linifolia L., also as *Teline linifolia* (L.) Webb & Berth.
G. microcephala Coss. & Durieu G. *monspessulana* (L.) L. A.S. Johnson, also as *Teline monspessulana* (L.) Koch
G. numidica Spach subsp. *numidica* Spach
G. pilosa L.
G. radiata (L.) Scop.
G. sagittalis L. as *Cytisus sagittalis*
G. sibirica Rchb.
G. spachiana Webb = *G. stenopetala*
G. supranubia Spach = *C. supranubius*
G. stenopetala Webb & Berth., as *Teline stenopetala* (Webb & Berth.)
G. tinctoria L.
G. tricuspidata Desf.

Geoffroea

G. decorticans (Hook. & Arn.) Burkart

Gliricidia

G. sepium (Jacq.) Walp.

Glycine

G. canescens F.J. Herm
G. clandestina Wendl.
G. falcata Benth.
G. max (L.) Merr. and subsp. *soja* (Siebold & Zucc.) H. Ohashi = *G. soja*
G. microphylla (Benth.) Tindale
G. schliebenii Harms = *Ophrestia radicosa* car *schliebenii* (Harms) Verdc.
G. soja Siebold & Zucc. = *G. max* subsp. *soja*
G. tabacina (Labill.) Benth.
G. tomentella Hayata
G. wightii (Wight & Arn.) Verdc. = *Neonotonia wightii*

Glycyrrhiza

G. acanthocarpa (Lindl.) J. Black
G. echinata L.
G. glabra L.
G. inflata Batelin
G. korshinskii Grigor
G. lepidota Pursh.
G. pallidiflora Maxim.
G. uralensis DC.

Gompholobium

G. amplexicaule Meisn.
G. confertum (DC.) Crisp, as *Burtonia conferta* DC.
G. huegelii Benth.
G. knightianum Lindl.
G, latifolium Sm.
G. marginatum R. Br.
G. minus Sm.
G. pinnatum Sm.
G. polymorphum R. Br.
G. scabrum Sm.
G. tomentosum Labill.
G. venustum R. Br.
G. virgatum DC.

Goodia

G. lotifolia Salisb.
G. pubescens Sims

Gueldenstaedtia

G. himalaica Baker, now *Tibetia himalaica*
G. multiflora Bunge = *G. verna*
G. verna (Georgi) A. Boriss.

Halimodendron

H. halodendron (Pall.) Voss

Hardenbergia

Hardenbergia comptoniana (Andrews) Benth.
H. monophylla (Vent.) Benth. = *H. violacea*
H. violacea (Schneev.) Stearn, as *H. monophylla*

Harpalyce

H. cubensis Griseb. Bécquer & Sprent, unpub. (2004)
H. macrocarpa Britton & Wilson. Bécquer & Sprent unpub. (2004)

Hebestigma

H. cubense (Kunth) Urb.

Hedysarum

H. aculeolatum Boiss.
H. alpinum L. and subsp. *americanum* (Michx.) Fedtsch.
H. boreale Nutt.
H. capitatum Burm.f. = *Sulla capitata*
H. carnosum Desf. = *Sulla carnosa*
H. caucasicum M. Bieb. = *H. hedysaroides*
H. coronarium L. = *S. coronaria*
H. flexuosum L. = *S. flexuosum*
H. glomeratum F. Dietr. = *S. glomerata*
H. hedysaroides (L.) Schinz & Thell.
H. humile L.
H. iomuticum B. Fedtsch.
H. mackenzii Richardson = *H. boreale* subsp. *mackenzii* (Richardson) S.L. Walsh
H. mongolicum Turcz. = *Corethrodendron fruticosum*
H. naudinianum Coo. & Durieu Muresu et al. (2008)
H. occidentale Greene
H. obscurum L. = *H. hedysaroides*
H. pallidum Desf. = *S. pallida*
H. polybotrys Haud-Mazz. Wei et al. (2008)
H. scoparium Fisch. & C.A. Mey = *C. scoparium*
H. spinosissimum L. and subsp *capitatum* (Rouy) Asch. & Graebn. Muresu et al. (2008) = *S. spinosissima*
H. vicioides Turcz. subsp. *japonicum* (Fedtsch) Choi & H. Ohashi, as *H. ussuriense* Schischk. & Kom.

Hesperolaburnum

H. platycarpum (Maire) Maire

Hippocrepis

H. areolata Desv., as *H. bicontorta*
H. comosa L.
H. emerus subsp. *emerus* (L.) Lassen, as *Coronilla emerus*
H. minor Munby S.
H. multisiliquosa L.
H. unisiliquosa L.

Hoita

H. macrostachya (DC) Rydb.
H. orbicularis (Lindl.) Rydb.

Hosackia

H. americana (Nutt.) Rydb.
H. parviflorus (Benth.) D. D. Sokoloff
H. pushiana Benth. = *H. americana*
H. subpinnata (Lag.) D.D. Sokoloff

Hovea

H. acutifolia Cunn.
H. chorizemifolia (Sweet) DC.
H. elliptica (Sm.) DC.
H. linearis (Sm.) R. Br.
H. longifolia R. Br.
H. pungens Benth.
H. purpurea Sweet
H. trisperma Benth.

Humularia

H. welwitschii (Taub.) Duvign.

Hylodesmum

H. glutinosum (Muhl. ex Willd.) H. Ohashi & R.R. Mill as *Desmodium glutinosum*
H. pauciflorum (Nutt.) H. Ohasi & R.R. Mill, as *D. pauciflorum*
H. oldhamii (Oliv.) H. Ohashi, as *D. oldhamii*
H. podocarpum (DC.) H. Ohashi & R.R. Mill, as *D. podocarpum*
H. repandum (Vahl) H. Ohasi & R.R. Mill, as *D. repandum*

Hymenocarpos

H. circinnatus (L.) Savi
H. cornicina (L.) Lassen = *Anthyllis cornicina* L.
H. lotoides (L.) Lassen = A. lotoides L.

Hymenolobium

H. alagoanum Ducke var. *parviflorum* H.C. de Lima and var. *algoanum* Ducke
H. heterocarpum Ducke
H. flavum Kleinh.
H. janeirense Kuhlmann
H. modestum Ducke
H. nitidum Benth.
H. petraeum Ducke

Hypocalyptus

H. coluteoides (Lam.) R. Dahlgren
H. oxalidifolius (Sims) Baill.
H. sophoroides (P.Bergius) Baill.

Indigastrum

I. argyroides (E.Mey.) Schrire, as *Indigofera argyroides*
I. burkeanum (Harv.) Schrire, as *I. burkeana*
I. costatum (Guill. & Perr.) Schrire and subsp. *macrum* (E. Mey.) Schrire, as *I. costata*
I. parviflorum (Wight & Arn) Schrire, as *I. parviflora*

Indigofera

I. acutisepala Baker f. = *I. zeyheri*
I. adenocarpa E. Mey.
I. adenoides Baker f.
I. alpina Eckl. & Zeyh., as *I. stipularis* Link, but synonymy doubtful
I. alternans DC.
I. anabaptista Steud. = *I. hochstetteri*
I. angustata E. Mey., as *I. stenophylla*
I. angustifolia L.
I. annua Milne-Redh. = *Microcharis annua*
I. antunesiana Harms
I. arenophila Schinz
I. argentea Burm.f.
I. argyroides E. Mey. = *Indigastrum argyroides*
I. arrecta A. Rich.
I. asperifolia Benth.
I. astragalina DC.
I. atriceps Hook. f. subsp. *atriceps* Hook.f.
I. atropurpurea Hornem.
I. auricoma E. Mey.
I. australis Willd.
I. bainesii Baker
I. bifrons E. Mey.
I. brachynema J.B. Gillett
I. brachystachya E. Mey.
I. brevidens Benth.
I. bungeana Walp.
I. burchellii DC.
I. candicans Aiton
I. candolleana Meisn.
I. capillaris Thunb.
I. cardiophylla Harv.
I. carlesii Craib.
I. caroliniana Mill.
I. cassioides DC.
I. cecili N.E. Br.
I. charlierana Schinz
I. chuniana F.P. Metcalf
I. circinella Baker f.
I. circinnata Harv.
I. colutea (Burm.f.) Merr. and var. *colutea* (Burm.f.) Merr.
I. comosa N.E.Br.
I. complicata Eckl. & Zeyh. Yates et al pers. comm. (2008)
I. cordifolia Roth
I. costata Guill. & Perr. subspp. *gonioides* (Baker) J.B. Gillett and *macra* (E. Mey.) J.B.Gillett = *Indigastrum costatum*
I. cryptantha Harv. and vars. *cryptantha* Harv. and *occidentalis* Baker f.
I. cuneata Oliv.
I. cuneifolia Eckl. & Zeyh.
I. cylindracea Wall. ex Baker
I. cytisoides Thunb.
I. daleoides Harv.
I. decora Lindl.
I. delagoaensis J.B.Gillett
I. demissa Taub.
I. dendroides Jacq.
I. denudata Thunb.
I. digitata Thunb.

I. dimidiata Walp.
I. dosua Buch.-Ham.
I. dregeana E. Mey
I. dyeri Britten
I. egens N.E. Br.
I. emarginella A. Rich.
I. enneaphylla L.
I. eriocarpa E. Mey.
I. erythrogramma Baker
I. evansiana Burtt. Davy
I. eylesiana J.B. Gillett
I. fanshawei J.B. Gillett
I. filicaulis Eckl. & Zeyh.
I. filiformis Thunb.
I. filipes Harv.
I. flavicans Baker
I. foliosa E. Mey.
I. fortunei Craib.
I. frutescens L.f.
I. fulvopilosa Brenan
I. gairdnerae Baker f.
I. galegoides DC.
I. garckeana Vatke
I. gerardiana R. Grah.
I. gerrardiana Harvey = *I. heterantha*
I. glandulosa Willd.
I. glaucescens Eckl. & Zeyh.
I. glomerata E. Mey.
I. griseoides Harms
I. hamiltonii Graham ex Duthie & Prain
I. hebepetala Benth. ex Baker
I. hedyantha Eckl. & Zeyh.
I. hendecaphylla Jacq., as *I. endecaphylla*
I. hermanus XXXXXX Yates et al. pers. comm. (2008)
I. heterantha Brandis and var. *gerardiana* (Wall.) ex Baker) Ali
I. heterophylla Thunb.
I. heterotricha DC.
I. heudelotii Baker var *heudelotii*
I. hewittii Baker f.
I. hilaris Eckl. & Zeyh.
I. hirsuta L.
I. hispida Eckl. & Zeyh.
I. hochstetteri Baker, as *I. anabaptista*
I. holubii N.E.Br.
I. humifusa Eckl. & Zeyh.
I. hirsuta L.
I. incana Thunb.
I. incarnata Nakai
I. ingrata N.E.Br.
I. inhambanensis Klotzsch
I. kirilowii Wied-Nuew.
I. langebergensis L. Bolus
I. laxiracemosa Baker f., as *I. mucronata*
I. lespedezioides Kunth
I. linnaei Ali
I. linifolia (L.f.) Retz.
I. linnaei Ali
I. litoralis Chun & T.C. Chen
I. livingstoniana J.B. Gillett
I. lobata J.B. Gillett = *Microcharis latifolia* Benth.
I. longepedicellata J.B. Gillett
I. longibarbata Engl.
I. longipes N.E. Br.
I. lupatana Baker f.
I. lyallii subsp. *lyallii* Baker
I. macrophylla Schumach.
I. macrostachya Willd.
I. malacostachys Benth.
I. maritima Baker
I. mauritania (L.) Thunb., as *I. coriacea* var. *cana*
I. melanadenia Harvey
I. meyeriana Eckl. & Zeyh.
I. microcarpa Desv.
I. mimosoides Baker vars. *mimosoides* Baker and *rhodesica* Baker f.
I. miniata Ortega
I. mischocarpa Schltr.
I. mollicoma N.E.Br.
I. monantha Baker f.
I. neglecta N.E. Br. = *I. spicata*
I. nigromontana Eckl. & Zeyh.
I. nummulariifolia (L.) Alston, as *I. echinata*
I. oblongifolia Forssk.
I. ormocarpoides Baker
I. ovata Thunb.
I. oxalidea Baker
I. oxytropis Harv.
I. oxytropoides Schltr.
I. paniculata Pers. subsp. *gazensis* (Baker f.) J.B. Gillett
I. podophylla Harv.
I. poliotes Eckl. & Zeyh.
I. pongolana N.E. Br.
I. porrecta Eckl. & Zeyh.
I. potaninii Craib
I. pratensis F. Muell.
I. praticola Baker f.
I. pretoriana Harms
I. procumbens L.
I. prostata Willd.
I. pseudo-indigofera (Merxm.) J.B. Gillett = *Microcharis galpinii*
I. pseudotinctoria Matsum.
I. psoraleoides L.
I. pulchra Willd.
I. purpurea Steud.
I. rautanenii Baker f.
I. reducta N.E. Br.
I. rehmannii Baker f.
I. reticulata Franch.
I. retroflexa Baill. = *I. trita* sub sp *scabra*
I. rhynchocarpa Baker var. *rhynchocarpa* Baker
I. rhytidocarpa Harv. and subsp. *rhytidocarpa* Harv.
I. richardsiae J.B. Gillett = *Microcharis angolensis*
I. ripae N.E. Br.
I. rostrata Bolus
I. sanguinea N.E. Br.
I. schimperi Jaub. & Spach
I. schinzii N.E. Br.
I. senegalensis Lam.
I. sessilifolia DC.
I. setiflora Baker
I. sordida Harv.
I. sphaerocarpa A. Gray
I. spicata Forssk., as *I. neglecta*
I. spinescens E. Mey.
I. stenophylla Eckl. & Zeyh., as *I. angustata*

I. stricta L.f.
I. strobilifera (Hochst.) Baker subsp. *strobilifera* (Hochst.) Baker
I. subcorymbosa Baker
I. subulifera var. *subulifera* Baker
I. suffruticosa Mill.
I. sulcata DC.
I. swaziensis Bolus and var. *perplexa* (N.E. Br.) J.B. Gillett
I. tenuis Milne-Redh. and subsp. *major* J.B. Gillett
I. tenuissima E. Mey.
I. tetragonoloba E. Mey.
I. tinctoria L. and var. *arcuata* J.B. Gillett
I. tomentosa Eckl. & Zeyh.
I. torulosa E. Mey.
I. trifoliata L.
I. tristis E. Mey.
I. tristoides N.E. Br.
I. trita L.f., as *I. subulata* and *I. retroflexa* and *I. trita* subsp. *subulata* (Poir.) Ali
I. velutina E. Mey.
I. vicioides Jaub. & Spach vars. *rogersii* (R.E. Fries) J.B. Gillett and *vicioides* Jaub. & Spach
I. viscidissima subsp. *viscidissima* Baker
I. welwitschii Baker var. *remotiflora* (Baker F.) Cronq. = *Microcharis remotiflora*
I. wildiana J.B. Gillett
I. williamsonii (Harv.) N.E. Br.
I. woodii Bolus
I. zeyheri Spreng.
I. zollingeriana Miq., as *I. teysmanni*

Inocarpus

I. fagifera (Parkinson) Fosberg, R. Leakey, pers. comm. (2004)

Isotropis

I. artopurpurea F. Muell.
I. cuneifolia (Sm.) B.D. Jackson
I. juncea Turcz.

Jacksonia

J. capitata Benth., as *J. umbellata*
J. dilatata Benth.
J. floribunda Endl.
J. furcellata (Bonpl.) DC.
J. hakeoides Meisn.
J. horrida DC.
J. scoparia Sm.
J. sericea Benth.
J. spinosa (Labill.) Sm.
J. sternbergiana Benth.
J. umbellata Turcz. = *J. capitata*

Kennedia

K. beckxiana F. Muell.
K. carinata (Benth.) Domin
K. coccinea Vent.
K. eximia Lindl.
K. glabrata (Benth.) Lindl.
K. macrophylla (Meisn.) Benth.
K. microphylla Meisn.
K. nigricans Lindl.
K. prorepens F. Muell.
K. prostrata R. Br.
K. retrorsa Hemsl.
K. rubicunda (Schneev.) Vent.
K. stirlingii Lindl.

Kotschya

K. capitulifera (Baker) J. Dewit & Duvign.
K. lutea (Porteres) Hepper Diabate et al. (2005)
K. ochreata (Taub.) Dewit & P.A. Duvign. var. *ochreata* Diabate et al. (2005)
K. scaberrima (Taub.) Wild
K. speciosa (Hutch.) Hepper
K. strigosa (Benth.) J. Dewit & Duvign.
K. strobilantha (Baker) Dewit & P.A. Duvign.
K. thymodora (Baker f.) Wild subsp. *thymodora* (Baker f.) Wild

Kummerowia

K. stipulacea (Maxim.) Schindl., as *Lespedeza stipulacea* (Thunb.) Maxim.
K. striata (Thunb.) Schindl., as *L. striata* (Thunb.) Maxim. Hook. & Arn.

Lablab

L. purpureus subsp. *uncinatus* Verdc.

Laburnum

L. alpinum (Mill.) Bercht. & J.S. Presl.
L. anagyroides Medik.

Lamprolobium

L. fruticosum Benth.

Lathyrus

L. alatus Kom.
L. angulatus L.
L. annuus L.
L. aphaca L.
L. articulatus L. = *L. clymenum*
L. blepharicarpus Boiss.
L. brachycalyx Rydb.
L. cicera L.
L. clymenum L., also as *L. articulatus*
L. crassipes Gillet ex Hook. & Arn. = *L. pusillus*
L. davidii Hance
L. emodii (Fritsch) Ali

L. eucosmus F.K. Butters & St. John
L. garminifolius (S. Watson) T.G. White
L. hierosolymitanus Boiss.
L. hirsutus L.
L. humilis (Ser.) Spreng.
L. inconspicuus L.
L. japonicus Willd. and subsp. *maritimus* (L.) P. Ball, as *L. maritimus*
L. jepsonii Greene
L. laevigatus (Waldst. & Kit.) Gren. and subsp. *occidentalis* (Fisch. & C. Mey.) Breist.
L. laszwertii var. *leucanthus* (Rydb.) Dorn.
L. latifolius L.
L. linifolius (Reichard) Bassler, as *L. montanus*
L. littoralis (Nutt.) Endl.
L. luteus (L.) Peterm. = *L. laevigatus* subsp. *occidentalis*
L. magellanicus Lam.
L. maritimus (L.) Bigelow = *L. japonicus* subsp. *maritimus*
L. marmoratus Boiss. & Blanche
L. montanus (L.) Bernh. = *L. linifolius*
L. nevadensis S. Watson
L. niger (L.) Bernh.
L. nissolia L.
L. numidicus Batt. Zakhia et al. (2006)
L. ochraceus Kitt
L. ochroleucus Hook.
L. ochrus (L.) DC.
L. odoratus L.
L. ornatus Orr. & A. Gray = *L. polymorphus* subsp. *polymorphus*
L. palustris L. and var. *linearifolius* Ser.
L. pisiformis L.
L. polymorphus subsp. *polymorphus* Nutt.
L. pratensis L.
L. pseudocicera Pamp.
L. pusillus Elliott, also as *L. crassipes*
L. sativus L.
L. sphaericus Retz.
L. sylvestris L.
L. szowitsii Boiss.
L. tingitanus L.
L. tuberosus L.
L. venosus Willd.
L. vernus (L.) Bernh.

Latrobia

L. hirtella (Turcz) Benth.

Lebeckia

L. ambigua (L.) Thunb. Phalane et al. (2008)
L. cinerea E. Mey. Yates et al., pers. comm. (2008)
L. cytisoides Thunb. = *Calobota cytisoides* Yates et al, pers. comm. (2008)
L. gracilis Eckl. & Zeyh. Yates et al., pers. comm. (2008)
L. halenbergensis erxz. & A. Schreib. Yates et al, pers. comm. (2008)
L. linearifolia E. Mey. = *C. linearifolia*
L. meyeriana Eckl. & Zeyh. Phalane et al. (2008)
L. multiflora E. May = *C. sericea* Phalane et al. (2008)
L. pauciflora Eckl. & Zeyh.
L. plukenetiana E. Mey.
L. pungens Thunb. = *C. pungens* Phalane et al. (2008)
L. sepiaria Thunb. Phalane et al. (2008)
L. sepicuria (L.) Thunb. Phalane et al. (2008)
L. sericea Thunb. = *C. thunbergii*
L. simsiana Eckl. & Zeyh.
L. spinescens Harv. = *C. spinescens*
L. wrightii (Harv.) Bolus

Lembotropis

L. nigricans (L.) Griseb., as *Cytisus nigricans*

Lens

L. culinaris Medik.
L. ervoides (Brign.) Grande Athar
L. esculenta Moench = *L. culinaris*
L. nigricans (M. Bieb.) Godr.
L. orientalis (Boiss.) Schmalh. Athar

Leptoderris

L. brachyptera (Benth.) Dunn Diabate et al. (2005)
L. fasciculata (Benth.) Dunn Diabate et al. (2005)
L. nobilis (Baker) Dunn

Leptosema

L. chambersii F. Muell., as *Brachysema chambersii*

Lespedeza

L. angustifolia (Pursh.) Elliott
L. bicolor Turcz. and var. *japonica* Nakai
L. buergeri Miq.
L. capitata Michx.
L. chinensis G. Don
L. cuneata (Dumont) G. Don
L. cyrtobotrya Miq.
L. davidii Franchet Wei et al. (2003)
L. daurica (Laxm.) Schindl.
L. divaricata (Nakai) T.B. Lee
L. floribunda Bunge
L. formosa (Vogel) Koehne
L. frutescens (L.) Britton = *L. intermedia*
L. fruticosa (L.) Britton

L. hedysaroides (Pall.) Kitagawa = *L. juncea*
L. hirta (L.) Hornem.
L. homoloba Nakai
L. intermedia (S. Watson) Britton
L. japonica L.H. Bailey
L. juncea (L.f.) Pers.
L. latissima Nakai = *L. cuneata* var *serpens* (Nakai) Ohwi
L. leptostachya A. Gray
L. maximowczii C.K. Schneider
L. pilosa Siebold & Zucc.
L. procumbens Michx.
L. repens (L.) Barton
L. schlindleri Lév.
L. sericea (Thunb.) Benth.
L. sieboldi Miq. = *L. thunbergii* (DC.) Nakai
L. stipulacea Maxim. = *Kummerowia stipulacea*
L. striata Maxim. = *Kummerowia striata*
L. stuevei Nutt.
L. tomentosa (Thunb.) Siebold ex Maxim.
L. thunbergii (DC.) Nakai
L. villosa Pers. = *L. tomentosa*
L. violacea (L.) Pers.
L. virgata DC.
L. virginica (L.) Britton

Lessertia

L. affinis Burtt Davy
L. annularis Burch.
L. benguellensis Baker f.
L. brachypus Harv.
L. brachystachya DC.
L. capitata E. Mey.
L. depressa Harv.
L. diffusa R. BR.
L. emarginata Schinz
L. excisa DC.
L. falciformis DC.
L. frutescens (L.) Goldblatt & J.C. Manning
L. harveyana L. Bolus
L. herbacea (L.) Druce
L. incana Schinz
L. inflata Harv.
L. macrostachya DC.
L. microphylla (Burch. ex DC.) Goldblatt & J.C. Manning
L. montana XXXXX Yates et al., pers. comm. (2008)
L. pauciflora Harv.
L. perennans DC. and var. *polystachya* (Harv.) L. Bolus
L. rigida E. Mey.
L. spinescens E. Mey.
L. stenoloba E. Mey.
L. stricta L. Bolus
L. thodei L. Bolus
L. tomentosa DC. van Wyk & Sprent (2008)

Liparia

Liparia calycina (L. Bolus), A.L. Schutte, as *Priestleya calycina*
Liparia hirsuta Thunb., as *P. hirsuta*
L. parva Vogel ex Walp
L. splendens L.
Liparia vestita Thunb., as *P. vestita*

Lonchocarpus

L. atropurpureus Benth. Parker (2004)
L. bussei Harms = *Philenoptera bussei*
L. campestris Mart. ex Benth.
L. capassa Rolfe = *Philenoptera violacea* (Klotsch) Schrire
L. constrictus Pittier González-Ruiz et al. (2008)
L. costatus Benth.
L. cultratus (Vell.) A.M.G. Azevedo & H.C. Lima
L. domingensis (Pers.) DC. = *L. sericeus*
L. discolor Huber = *L. heptaphyllus*
L. eriocarinalis Micheli S Altomirano-Hernandez et al. (2004)
L. ernestii Harms = *L. macrocarpus*
L. filipes Benth.
L. guilleminianus (Tul.) Malme = *L. cultratus*
L. heptaphyllus (Poir.) DC.
L. latifolius (Willd.) DC. = *L. heptaphyllus*
L. leucanthus Burkart = *L. campestris*
L. macrocarpus Benth., as *L. ernestii*
L. muehlbergianus Hassl.
L. negrensis Benth. = *Deguelia negrensis* (Benth.) Taub.
L. nelsii (Schinz) Heering & Grimme = *Philenoptera nelsii* (Schinz) Schrire
L. nitidus (Vogel) Benth.
L. pentaphyllus (Poir.) = *L. heptaphyllus*
L. punctatus Kunth
L. roseus (Mill.) DC = *L. punctatus*.
L. sericeus (Poir.) Kunth
L. spruceanus Benth. = *Deguelia spruceana*
L. violaceus Kunth
L. virgilioides (Vogel) Benth = *L. punctatus*.

Lotononis

L. acutiflora Benth. Yates et al., pers. comm. (2008)
L. adpressa N.E.Br., as *L. sericoflora*
L. angolensis Baker
L. arenicola De Wild. Yates et al., pers. comm. (2008)
L. azurea Benth.
L. bainesii Baker
L. benthamiana Dummer
L. bolusii Dummer Yates et al., pers. comm. (2008)
L. brachycantha Harms Yates et al., pers. comm. (2008)
L. calycina (E. Mey.) Benth. and var. *hirsutissima* Dümmer

L. carnea B-E van Wyk Yates et al., pers. comm. (2008)
L. carinata (E. Mey.) Benth.
L. corymbosa Benth.
L. crumaniana Benth.
L. cytisoides Benth.
L. decumbens (Thunb.) B-E van Wyk
L. depressa Eckl. & Zeyh.
L. delicata (Baker f.) Polhill Yates et al., pers. comm. (2008)
L. digitata Harv.
L. divaricata (Eckl. & Zeyh.) Benth.
L. eriantha Benth.
L. falcata (E. Mey.) Benth.
L. florifera Dümmer = *L. carinata*
L. foliosa Bolus
L. fruticoides B-E van Wyke
L. glabra (Thunb.) D. Dietr.
L. globulosa XXXXX Yates et al., pers. comm. (2008)
L. hirsuta (Thunb.) D. Dietr.
L. involucrata (Bergius) Benth. and sub sp. *peduncularis* (E. Mey.) B-E van Wyk
L. laxa Eckl. & Zeyh. and var. *multiflora* Dümmer
L. lenticula (E. Mey.) Benth.
L. leobordea Benth. = *L. platycarpa*
L. leptoloba Bolus
L. listii Polhill, as *L. heterophylla* E. Mey.
L. longiflora Bolus
L. lotononoides (Scott Elliot) B.-E van Wyk, as *B. lotononoides* Scott Elliot
L. macrocarpa Eckl. & Zeyh.Yates et al. (2007)
L. macrosepala Conrath
L. marlothii Engl. Ardley et al. (2008)
L. maximilliana Schltr.ex De Wild.
L. minima B-E van Wyk Ardley et al. (2008)
L. mucronata Conrath
L. namaquensis (Bolus) B.-Evan Wyk van Wyk & Sprent (2008)
L. orthorrhiza Conrath
L. oxyptera (E.Mey.) Benth. Yates et al, pers. comm. (2008)
L. parviflora (P.J. Bergius) D. Dietr.
L. platycarpa (Viv.) Pic. Serm.
L. polycephala (E.Mey.) Benth.
L. prostrata (L.) Benth.
L. pulchella (E. Mey.) B.-E. van Wyk, as *B. tenuifolia* var. *pulchella* (E. Mey.) Harv.
L. pulchra Dummer Yates et al., pers. comm. (2008)
L. pungens Eckl. & Zeyh.
L. quinata (Thunb.) Benth.
L. rabenaviana Dinter & Harms Yates et al., pers. comm. (2008)
L. serpentinicola H. Wild
L. solitudinus DummerYates et al. (2007)
L. sparciflora (E. May) B-E van Wyk Yates et al., pers. comm. (2008)
L. speciosa Hutch. Yates et al., pers. comm. (2008)
L. steingroeveriana Dümmer
L. stipulosa Baker f.
L. stricta (Eckl. & Zeyh.) B-E van Wyk
L. strigillosa (Merxm. & A. Schreib.) A. Schreib.
L. subulata B-E van Wyk, Ardley et al. (2008)
L. tenella Eckl. & Zeyh.
L. trichopoda (E. Mey.) Benth.
L. wilmsii Dummer

Lotus

L. alamosanus (Rose) H. Gentry
L. alpinus (Ser.) Sschleich. ex Ramond
L. americanus (Nutt.) Bisch. = *L. purshianus*
L. angustissimus L.
L. arabicus L.
L. arenarius Brot.
L. argenteus Webb & Berth. = *L. polyphyllus*
L. australis Andrews
L. castellanus Boiss. & Reuter, as *L. subbiflorus*
L. coccineus Schldl.
L. collinus (Boiss.) Heldr.
L. conimbricensis Brot
L. conjugatus L., as *T. conjugatus* (L.) Link and subsp. *requienii* (Sang.) Greuter, as *T. requenii* (Mauri ex Sang.) Sang.
L. corniculatus L. and var. *japonicus* Regel
L. crassifolius (Benth.) Greene
L. creticus L.
L. cruentus Court
L. cystisoides L.
L. discolor E. Mey. and subsp. *mollis* J.B. Gillett
L. edulis L.
L. formosissimus Greene
L. frondosus Freyn = *L. corniculatus*
L. glaber Mill., as *L. tenuis*
L. glinoides (Del)
L. grandiflorus (Benth.) Greene
L. greenei Kearney & Peebles
L. halophilus Boiss. & Spruner, as *L. pusillus*
L. hispidus Desf. + *L. suaveolens*
L. humistratus (Benth.) Greene
L. junceus (Benth.) Greene = *Syrmatium junceum* Greene
L. lamprocarpus Boiss. = *L. palustris*
L. major Scop. = *L. corniculatus*
L. maritimus L., = *T. maritimus* (L.) Roth
L. maroccanus Ball
L. mearnsii (Britton) Greene

L. micranthus Benth., as *Hosackia parviflora* Benth., = *Acmispon parviflorus*
L. namulensis Brand
L. nevadensis (S. Watson) Greene
L. nudiflorus (Torr. & A. Gray) Greene = *Ottleya strigosa*
L. oblongifolius (Benth.) Greene, also as *L. torreyi*
L. ornithopodioides L.
L. oroboides (Kunth.) Kearney & Peebles = *Ottleya oroboides* (Kunth) D.D. Sokoloff Qian & Parker (2002)
L. palaestinus (Boiss. & Blanche) Blatter, = *Tetragonobolus palestinus* Boiss.
L. palustris Willd., as *L. lamprocarpus*
L. parviflorus Desf.
L. pedunculatus Cav
L. peregrinus L.
L. pinnatus Hook.
L. polyphyllus E.D. Clarke
L. preslei Ten
L. purpureus Webb = *Tetragonolobus purpureus* Moench
L. purshianus Lindl. (Ottley), as *Hosackia americana* (Nutt.) Piper and *H. pilosa* Nutt.
L. pusillus Medik. = *L. halophilus*
L. requieni Mauri = *L. conjugatus* subsp. *requenii*
L. rigidus (Benth.) Greene
L. rubellus (Torr. & A. Gray) Greene = *Ottleya strigosa*
L. salsuginosus Greene
L. schoelleri Schweinf.
L. scoparius (Torr. & A. Gray) Ottley = *Syrmatium glabrum* Vogel
L. sessilifolius DC.
L. spectabilis Choisy = *Dorycnium spectabile* (Choisy ex Ser.) Webb & Berthel.
L. strictus Fisch. & C. Mey.
L. strigosus (Torr. & A. Gray) Greene
L. suaveolens Pers. = *L. hispidus*
L. subbiflorus Lag.
L. tenuis Waldst. & Kit. ex Willd. = *L. glaber*
L. tetragonolobus L.
L. torreyi (A. Gray) Greene = *L. oblongifolius*
L. uliginosus Schkuhr
L. weilleri Maire
L wildii J.B.Gillett
L. wrangelianus Fisch. & Mey. also as *Tetragonolobus subpinnata* Torr. & A. Gray = *Acmispon wrangelianus*

Lupinus

L. affinis J. Agardh.
L. albicaulis Douglas
L. albifrons Benth.
L. albus L. and subsp. *albus* L.
L. ananeanus Ulbr.
L. angustiflorus Eastw.
L. angustifolius L.
L. arboreus Sims
L. arbustus Douglas ex Lindl.
L. arcticus S. Watson
L. argenteus Pursh
L. arizonicus S. Watson
L. atlanticus Glads.
L. benthamii A.A. Heller
L. bicolor Lindl. and subspp. *microphyllus* (S. Watson) D. Dunn, *pipersmithii* (A.A. Heller) D. Dunn, *tridentatus* (Eastw.) D. Dunn, and *umbellatus* (Greene) D. Dunn
L. breweri A. Gray
L. caespitosus Torr. & A. Gray
L. campestris Schtdl. & Cham.
L. chamissonis Eschsch
L. concinnus J. Agardh
L. confertus Kellogg = *L. lepidus* var *confertus* (Kellogg) C.P. Sim
L. cosentinii Guss. C.E. Hughes pers. comm. (2007)
L. cumulicola Small C.E. Hughes pers. comm. (2007)
L. densiflorus Benth.
L. diffusus Nutt.
L. digitatus Forssk.
L. elegans Kunth
L. exaltatus Zucc.
L. flavoculatus A.A.Heller
L. formosus Greene
L. fulcratus Greene
L. grayi S. Watson
L. hartwegii Lindl. = *L. mexicanus*
L. harvardi S. Watson
L. heptaphyllus (Vell.) Hassl.
L. hirsutissimus Benth.
L. hirsutus L.
L. hispanicus Boiss. & Reuter
L. kingii S. Watson
L. latifolius Agardh subsp. *latifolius* Agardh
L. lepidus Lindl.
L leucophyllus Lindl.
L. luteus L.
L. meridianus Moritz ex C.P. Sim
L. mexicanus Cerv. ex Lag
L. micranthus Guss.
L. microcarpus Sims
L. montanus Kunth.
L. multiflorus Desr.
L. mutabilis Sweet
L. nanus Benth.
L. nootkatensis Sims
L. palaestinus Boiss.
L. perennis L. and var. *occidentalis* S. Watson
L. pilosus Murray
L. polyphyllus Lindl.
L. pubescens Benth.
L. pusillus Pursh subsp. *intermontanus* (A.A. Heller) D. Dunn
L. sabulosus A.A. Heller

L. sellulus Kellogg = *L. lepidus* var *sellulus* (Kellogg) Barneby
L. sericeus Pursh.
L. sparsiflorus Benth.
L. spectabilis Hoover
L. subcarnosus Hook.
L. succulentus K. Koch
L. texanus Hook.
L. vallicola A.A. Heller and subsp. *apricus* (Greene) D. Dunn
L. varius L. = *L. angustifolius* L.
L. villosus Willd.

Maakia

M. amurensis Rupr. and var. *buergeri* (Maxim.) C. Schneider

Machaerium

M. aculeatum Raddi
M. angustifolium Vogel = *M. isadelphum*
M arboreum (Jacq.) Vogel
M. brasiliense Vogel
M. ferox (Mart. ex Benth.) Ducke
M. firmum (Vell. Conc.) Benth.
M. floribundum Benth.
M. froesii Rudd
M. gracile Benth.
M. hirtum (Vell. Conc.) C. Stellfeld
M. incorruptuble Allemão
M. inundatum (Mart. ex Benth.) Ducke
M. isadelphum (E. Mey) Standl., as *M. angustifolium* Vogel
M. lunatum (L.f.) Ducke
M. madeirense Pittier)
M. microphyllum (E. Mey.) Standl. Parker (2003)
M. milleflorum Pittier
M. myrianthum Benth.
M. nyctitans (Vell. Conc.) Benth.
M. pedicellatum Vogel
M. quinata (Aubl.) Sandwith Moreira et al. (1992) and var. *quinata* (Aubl.) Sandwith
M. robinifolium (DC.) Vogel
M. scleroxylum Tul.
M. stipitatum (DC.) Vogel
M. triste Vogel
M. villosum Vogel

Macroptilium

M. atropurpureum (DC.) Urb.
M. bracteatum (Nees & Mart.) Maréchal & Baudet
M. erythroloma (Benth.) Urb., as *Phaseolus erythroloma*
M. gibbosifolium (Ortega) A. Delgado
M. gracile (Poepp. ex Benth.) Urb.
M. lathyroides (L.) Urb.
M. martii (Benth.) Maréchal & Baudet

Macrotyloma

M. africanum (Wilczek) Verdc.
M. axillare (E. Mey.) Verdc. and var. *glabrum* (E. Mey.) Verdc.
M. daltonii (Webb) Verdc.
M. densiflorum (Baker) Verdc.
M. geocarpum (Harms) Marechal & Baudet
M. maranguense (Taub.) Verdc., as *Dolichos taubertii* Baker f.
M. oliganthum (Brenan) Verdc.
M. rupestre (Baker) Verdc.
M. stipulosum (Baker) Verdc.
M. tenuiflorum (Micheli) Verdc., as *Dolichos baumannii* Harms
M. uniflorum (Taub.) Verdc.

Marina

M. parryi (A. Gray) Barneby, as *D. parryi* A. Gray

Mastersia

M. bakeri (Koord.) Baker

Medicago

M. aculeata Willd. (var. *aculeata* Willd.) = *M. doliata*
M. arabica (L.) Hudson
M. arborea L.
M. archducis-nicobi Sirj.
M. aschersonianaI Urb. = *M. laciniata* subsp. *aschersoniana*
M. blancheana Boiss.
M. caerulea Ledeb. = *M. sativa* subsp. *microcarpa* Urb.
M. cancellata M. Bieb.
M. carstiensis Jacq
M. ciliaris (L.) Krock. = *M. intertexta* subsp. *ciliaris*
M. constricta Durieu Béna et al. (2005)
M. coronata (L.) Béna et al. (2005)
M. disciformis DC.
M. doliata Carmign., as *M. aculeata*
M. edgeworthii Sirj., as *T. pubescens*
M. falcata L. = *M. sativa* subsp. *falcata* (L.) Arcang.
M. globosa C. Presl = *M. constricta*
M. granadensisi Willd.
M. hybrida (Pourret) Trautv., as *T. hybrida*
M. hypogaea E. Small, as *Factorovskya aschersoniana* (Urb.) Eig.
M. intertexta (L.) Mill. and subsp. *ciliaris* (L.) Heyne, as *M. ciliaris*

M. italica (Mill.) Fiori subsp. *tornata* (L.) Emb. & Maire = *M. tornata* subsp. *tornata*
M. laciniata (L.) Mill. and subsp. *schimperiana* (Hochst.) P. Fourn, as *M. aschersoniana*
M. littoralis Lois.
M. lupulina L.
M. marina L.
M. medicaginoides (Retz.) E. Small, as *Trigonella arcuata* and *T. cancellata*
M. minima (L.) Bartal. and var. *minima* (L.) Bartal.
M. monantha (C. Mey.) Trautv., as *T. monantha*
M. monspeliaca (L.) Trautv.
M. murex Willd.
M. noeana Bioss. Béna et al. (2005)
M. orbicularis (L.) Bartal.
M. orthoceras (Kar. & Kir.) Trautv., as *Trigonella orthoceras* Karelin & Kir
M. papillosa Boiss.
M. polyceratia (L.) Trautv.
M. polymorpha L. and vars. *brevispina* (Benth.) Heyn, *polymorpha* L. and *vulgaris* (Benth.) Shinn.
M. phrygia (Boiss. & Bal.) E. Small, as *Trigonella aurantica*
M. praecox DC.
M. radiata L. Béna et al. (2005)
M. rigidula (L.) All. and subsp. *agrestis* (Ten.) Ponert = *M. rigidula*
M. rotata Boiss.
M. rugosa Desr.
M. ruthenica Trautv.
M. sativa L. and subsp. *microcarpa* Urb., as *M. coerulea*
M. scutellata (L.) Mill.
M. soleirolii Duby
M. sphaerocarpa Bertol. = *M. murex*
M. tornata (L.) Mill. and subsp. *tornata* (L.) Mill., as *M. italica* subsp. *tornata*
M. truncatula Gaertner
M. turbinata (L.) All.

Melilotus

M. albus Medik.
M. altissimus Thuill.
M. caeruleus Desr. = *Trigonella coerulea* (L.) Ser.
M. caspius Gruner = *M. polonicus*
M. dentatus (Waldst. & Kit.) Pers.
M. gracilis DC. = *M. spicatus*
M. indicus (L.) All.
M. infestus Guss.
M. italicus (L.) Lam.
M. macrocarpa Coss. & Durieu
M. messanensis (L.) All. = *M. siculus*
M. neapolitanus Ten. = *M. sulcatus*
M. officinalis (L.) Pall. and subsp. *alba* (Medik.) H. Ohashi & Tateishi, as *M. alba*
M. polonicus (L.) Desr.
M. segetalis (Brot.) Ser.
M. siculus (Turra) B.D. Jacks.
M. speciosus Durieu
M. spicatus (Sm.) Breistr.
M. suaveolens Ledeb.
M. sulcatus Desf.
M. wolgicus Poir.

Melolobium

M. adenodes Eckl. & Zeyh.
M. aethiopicum (L.) Druce
M. alpinum Eckl. & Zeyh.
M. calycinum Benth.
M. candicans (E.Mey.) Eckl. & Zeyh.
M. exudens Harr. Yates et al. pers. comm. (2008)
M. humile Eckl. & Zeyh.
M. microphyllum (L.f.) Eckl. & Zeyh.
M. obcordatum Harv.

Microcharis

M. angolensis Baker
M. annua (Milne-Redh.) Schrire
M. remotiflora (Baker f.) Schrire

Millettia

M. dinklagei Harms Diabate et al. (2005)
M. dubia De Wild.
M. duchesnei De Wild.
M. extensa (Benth.) Baker
M. ferruginea (Hochst.) Baker
M. glaucescens Kurz
M. grandis (E.Mey.) Skeels
M. megasperma Benth. = *Callerya megasperma*
M. harmsiana De Wild.
M. japonica (Siebold & Zucc.) A. Gray
M. laurentii de Wild.
M. pinnata (L.) G. Panigrahi, as *Pongamia pinnata*
M. rhodantha Baill. Diabate et al. (2005)
M. stuhlmannii Taub.
M. thonningii (Schum. & Thonn.) Baker
M. usaramensis Taubert subsp. *australis* J.B. Gillett
M. zechiana Harms Diabate et al. (2005)

Mirbelia

M. dilatata R.Br.
M. floribunda Benth.
M. ovata Meisn.
M. oxylobioides F. Muell.
M. pungens G. Don
M. ramulosa (Benth.) C. Gardner

M. rubiifolia (Andrews) G. Don
M. spinosa Benth.

Montigena

M. novae-zelandiae (Hook. f.) Heenan, as *Swainsona novae-zelandiae*

Mucuna

M. aterrima (Piper & Tracy) Merr.
M. bennetti F. Muell.
M. birdwoodiana Tutcher
M. bracteata DC.
M. capitata Wight & Arn. = *M. pruriens* var. *utilis* (Wall. ex Wight) Baker ex Burck
M. coriacea Baker and subsp. *irritans* (Burtt Davy) Verdc.
M. deeringiana (Bort) Merr. = *M. pruriens* var. *utilis*
M. diabolica Backer ex Keuch.
M. flagellipes Hook. f.
M. gigantea (Willd.) DC.
M. hainensis subsp. *multilamellata* Wilmot-Dear
M. monosperma DC.
M. nigricans (Lour.) Steud. = *M. hainensis* subsp. *multilamellata* Wilmot-Dear
M. novoguineensis Scheff.
M. poggei Taub. (taken to be the var. *pesa* (De Wild.) Verdc.)
M. pruriens (L.) DC. and vars. *pruriens* (L.) DC. and *utilis* (Wight) Burck
M. rostrata Benth.
M. sempervirens Hemsl.
M. sloanei Fawc. & Rendle
M. urens (L.) Medik.
M. utilis Wight = *M. pruriens* var. *utilis* (Wall. ex Wight) Baker ex Burck

Muelleranthus

M. trifoliolatus A. Lee

Mundulea

M. sericea (Will.) A. Chev.

Neonotonia

N. wightii (Wight & Arn.) Lackey, as *Glycine wightii*

Neorautanenia

N. amboensis Schinz
N. brachypus (Harms) C.A. Smith = *N. amboensis*

Neorudolphia

N. volubilis Brandegee, as *Rudolphia volubilis* Willd.

Ohwia

O. caudata (Thunb. DC.) H. Ohashi, as *Desmodium caudatum*

Olneya

O. tesota A. Gray

Onobrychis

O. arenaria (Kit.) DC. and subsp. *sibirica* (Besser) P. Ball
O. argentea Boiss.
O. biebersteinii Sirj.
O. caput-galli (L.) Lam.
O. chorissanica Bunge
O cornuta (L.) Desv. S. Amrani pers. comm. to J.H. Kirkbride (2006)
O. crista-galli (L.) Lam.
O. cyri Grossh.
O. grandis Lipsky
O. kabylica Maire
O. micrantha Schrenk
O. paucidentata Pomel.
O. petrea (Willd.) Fischer
O. squarrosa Viv. = *O. crista-galli*
O. transcaucasia Grossh.
O. viciifolia Scop.

Ononis

O. alba Poir.
O. alopecuroides L.
O. antennata Pomel subsp. *antennata* Pomel
O. arvensis L.
O. columnae All., = *O. pusilla*
O. cristata Mill.
O. euphrasiaefolia Desf.
O. fruticosa L.
O. inermis Pall.
O. mitissima L.
O. natrix L.
O. officinalis L.
O. pusilla L., as *O. columnae*
O. reclinata L.
O. repens L. = *O. spinosa* subsp. *procurrens*
O. rotundifolia L.
O. serrata Forssk.
O. spinosa L. and subsp. *procurrens* (Walraven) Briq., as *O. repens*
O. subspicata Lag.
O. vaginalis M. Vahl
O. variegata L. S. Amrani pers. comm. to J.H. Kirkbride (2006)
O. viscosa L.

Oogeinia

O. dalbergioides Benth, as *Desmodium oujeinense*

Ophrestia

O. oblongifolia E. Mey.) H.M.Forbes

O. radicosa (A. Rich.) Verdc.
O. unifoliolata (Baker f.) Verdc.
O. retusa H.M.Forbes = *O. oblongifolia*

Orbexilum

O. onobrychis (Nutt.) Rydb. = *Psoralea onobrychis*
O. peduculatum var. *gracile*, (Torr. & A. Gray) Grimes as *O. pedunculatum* (Mill.) Rydb.
O. simplex (Nutt.) Rydb. = *Psoralea simplex*

Ormocarpum

O. cochinchinense (Lour.) Merr.
O. kirkii S. Moore
O. trichocarpum (Taub.) Harms
O. sennoides (Willd.) DC.

Ormosia

O. apiculata H.Y.Chen
O. arborea (Vell. Conc.) Harms
O. coarctaca G. Jacks.
O. coccinea (Aubl.) G. Jacks.
O. costulata (Miq.) Kleinhoonte
O. coutinhoi Ducke
O. discolor Benth.
O. emarginata (Hook & Arn.) Benth.
O. excelsa Benth.
O. fastigiata Tul.
O. flava (Ducke) Rudd
O. glauca Wall
O. henryi Prain
O. holerythra Ducke
O. hosei Hemsl. & E.H. Wilson
O. krugii Urb.
O. macrocalyx Ducke
O. melanocarpa Kleinhoonte
O. monosperma (Sweet) Urb.
O. nitida Vogel
O. nobilis Tul.
O. paraensis Ducke
O. pinnata (Lour.) Merr.
O. semicastrata Harms
O. sumatrana (Miq.) Prain
O. xylocarpa Merr. & H.Y. Chen

Ornithopus

O. compressus L.
O. isthmocarpus Coss., as *O. sativus* subsp. *isthmocarpus* (Coss.) Dostál
O. micranthus (Benth.) Arechav.
O. perpusillus L.
O. pinnatus (Mill.) Druce

Otholobium

O. augustifolia XXXXXX Yates et al. pers. comm. (2008)
O. candicans (Eckl. & Zeyh.) C.H. Stirt., as *Psoralea candicans* Eckl. & Zehy.
O. bracteolatum Eckl. & Dyer, Stirton & Sprent, 2008
O. decumbens (Aiton) C.H. Stirt., as *P. decumbens* Aiton
O. foliosum (Oliv.) C.H. Stirt., as *P. foliolosa* Oliv.
O. fruticans (L.) C.H. Stirt., as *P. fruticans* (L.) Bruce
O. glandulosum (L.) J.W. Grimes
O. hirtum (L.) C.H. Stirton Stirton & Sprent, 2008
O. rotundifolium (L.f.) C.H. Stirt., as *P. rotundifolia* L.
O. sericeum (Poir.) C.H. Stirt., as *P. tomentosa* Thunb.
O. striatum (Thunb.) C.H. Stirt.
O. virgatum (Burm f.) C.H. Stirton & Sprent (2008) unpub.
O. wilmsii (Harms) C.H. Stirt., as *P. wilmsii* Harms

Otoptera

O. burchellii DC.

Ottleya

O. strigosa (Nutt.) D.D. Sokoloff as *Lotus strigosa*
O. strigosa (Torr. & A. Gray) D.D. Sokoloff, as *L. nudiflorus* and *L. rubellus*

Oxylobium

O. atropurpureum Turcz. = *Nemcia leakeana*
O. capitatum Benth. = *Nemcia capitata*
O. ellipticum (Vent.) R.Br.
O. lanceolatum (Vent.) Druce = *Callistachys lanceolata*
O. parviflorum Benth. = *Gastrolobium parviflorum*
O. reticulatum Meisn. = *Nemcia reticulata*
O. robustum J. Thompson
O. scandens (Sm.) Benth.

Oxyrhynchus

O. volubilis Brandegee

Oxytropis

O. anertii Nakai
O. arctica R.Br.
O. arctobia Bunge = *O. nigrescens* var. *uniflora*
O. borealis DC. var *borealis*
O. campanulata Vassilez
O. campestris (L.) DC. and vars. *chartacea* (Fassett) Barneby, as *O. chartacea*; *columbiana* (St.John) Barneby, as *O. columbiana*; *gracilis* (Nelson) Barneby, as *O. gracilis*; *varians* (Rydb.) Barneby, as *O. varians* and subsp. *sordida* (Willd.) Hart. f., as *O. sordida*
O. carpatica R.Uechtr.
O. deflexa (Pall.) DC. and vars. *foliolosa* (Hook.) Barneby, as *O. foliolosa*, and *sericea* Torr. & A.Gray

O. glabra DC. var. elongata (Nelson) Schumann
O. halleri Bunge ex W.D.J. Koch
O. kansuensis Bunge
O. koyukukensis A.E. Porsild = *O. arctica* var. *koyukukensis* (A.E. Porsild, S.L. Walsh
O. lamberti Pursh
O. lapponica (Wahlenb.) Gay
O. leucantha (Pell.) Pers.
O. maydelliana Trautv.
O. melanocalyx Bunge
O. mollis A.Gray = *O. viscida*
O. neglecta Ten
O. nigrescens (Pall.) DC.
O. oreophila A. Gray
O. pilosa (L.) DC.
O. pyrenaica Godr. & Gren. = *O. neglecta*
O. riparia Litv.
O. scammaniana Hultén
O. sericea Nutt.
O. splendens Douglas ex Hook
O. viscida Torr. & A. Gray and var. *subsucculenta* (Hook.) Barneby = *O. borealis* var. *borealis*

Pachyrhizus

P. angulatus DC. = *P. erosus*
P. erosus (L.) Urb.
P. ferrugineus (Piper) M. Sørensen Rodriguez-Navarro et al. (2004),
P. tuberosus (Lam.) Spreng.

Paramachaerium

P. ormosioides (Ducke) Ducke

Parochetus

P. communis D. Don

Parryella

P. filifolia A.Gray

Pearsonia

P. aristata (Schinz) Dümmer
P. atherstonei Dümmer = *P. sessiliflora* subsp. *marginata*
P. cajanifolia (Harv.) Polhill subsp. *cryptantha* (Baker) Polhill
P. grandifolia (Bolus) Polhill subsp. *latebracteolata* (Dümmer) Polhill
P. marginata (Schinz) Dümmer var. *marginata* Dümmer = *P. sessiliflora* subsp. *marginata*
P. mesopontica Polhill
P. metallifera Wild
P. podalyriaefolia Dümmer = *P. sessilifolia* sub sp *marginata*
P. propinqua Dümmer = *P. sessilifolia* subsp. *marginata*
P. sessilifolia subspp. *filifolia* (Bolus) Polhill and *marginata* (Schinz) Polhill

Pediomelum

P. argophyllum (Pursh) Rydb.
P. esculentum (Pursh) Rydb.
P. subacaule (Torr. & A. Gray) Rydb.

Periandra

P. coccinea Benth.
P. mediterranea (Vell.) Taub.

Pericopsis

P. angolensis (Baker) van Meeuwen
P. elata (Harms) van Meeuwen
P. mooniana Thwaites

Petteria

P. ramentacea (Sieb.) C. Presl.

Phaseolus

P. aborigineus Burkart = *P. vulgaris* var. *aborigineus*
P. acutifolius A. Gray and var. *latifolius* Freeman
P. adenanthus G. Mey. = *Vigna adenantha* (G. Mey.) Maréchal et al.
P. angustifolius Roxb.
P. coccineus L.
P. diversifolia Pittier
P. dumosus Macfad.
P. filiformis Benth
P. lunatus L. var. *macrocarpus*
P. pauciflorus Benth. = *Strophostyles leiosperma* (Torr. & A. Gray) Piper
P. parvulus Greene
P. pedicellatus Benth.
P. pilosus Kunth = *Vigna lasiocarpa*
P. polystachyus (L.) Britton et al.
P. sublobatus Roxb. = *Vigna radiata* var. *sublobata* (Roxb.) Verdc.
P. viridissimus Ten. ex Miq. = *Vigna mungo* (L.) Hepper var. *mungo*
P. vulgaris L. and var. *aborigineus* (Burkart) Baudet

Philenoptera

P. bussei (Harms) Schrire, as *Lonchocarpus bussei*
P. nelsii (Schinz) Schrire, as *L. nelsii*
P. violacea (Klotzsch.) Schrire
P. wankieensis (Mendonca E.P. Sousa) Lock

Phyllodium

P. pulchellum (L.) Desv.
P. elegans (Lour.) Desv., as *Desmodium blandum* van Meuven

Phyllota

P. barbata Benth.
P. phylicoides Benth.
P. pleurandroides F. Muell.

Pickeringia

P. montana Torr. & A.Gray

Piptanthus

P. concolor Harrow ex Craib.
P. leiocarpus Stapf.
P. nepalense (Hook.) D. Don

Piscidia

P. piscipula (L.) Sarg.
P. grandiflora I.M. Johnst.

Pisum

P. sativum L. and subsp. *sativum* L., as *P. arvense*

Platycyamus

P. regnellii Benth.

Platylobium

P. formosum Sm.
P. obtusangulum Hook.

Platymiscium

P. duckei Huber = *P. trinitatis*
P. floribundum Vogel
P. paraensis Huber = *P. ulei*
P. pinnatum (Jacq.) Dugand
P. speciosum Vogel)
P. stipulare Benth.
P. trinitatis Benth.
P. ulei Harms

Platypodium

P. elegans Vogel

Podalyria

P. biflora (Retz.)Lam.
P. burchellii DC.
P. calyptrata (Retz.)Willd.
P. canescens E. Mey
P. cordata R.Br.
P. cuneifolia Vent.
P. glauca DC.
P. myrtillifolia Willd.
P. sericea R.Br.
P. velutina Benth.

Podolobium

P. alpestre (F. Muell.) Crisp & Weston, formerly *Oxylobium alpestre* F. Muell.
P. ilicifolium (Andrews) Crisp & Weston, formerly *Pultenaea ilicifolia* Andrews

Podolotus

P. hosackioides Royle ex Benth.

Poecilanthe

P. amazonica (Ducke) Ducke S.M. de Faria pers comm to J.H. Kirkbride (2006)
P. falcata (Vell. Conc.) Heringer, as *P. grandiflora*
P. grandiflora Benth., as *P. falcata*
P. hostmannii (Benth.) Amshoff
P. parviflora Benth.
P. ulei (Harms) Arroyo & Rudd

Poiretia

P. punctata Willd.

Poitea

P. punicea (Urb.) Lavin

Pseudarthria

P. hookeri Wight & Arn.
P. viscida Wight & Arn.

Pseudeminia

P. comosa (Baker) Verdc.

Pseudovigna

P. argentea (Willd.)Verdc.

Psophocarpus

P. lancifolius Harms
P. lukafuensis (De Wild.) R. Wilczek
P. palustris Desv.
P. scandens (Endl.) Verdc.
P. tetragonolobus (L.) DC.

Psoralea

P. acaulis Steven
P. aculeata L. Kanu et al. (2008)
P. adscendens F. Muell.
P affinis Eckl. & Zeyh.
P. alata (Thunb.) T.M. Salter
P. aphylla L.
P. argophylla Pursh
P. asarina (P. Bergius) T.M. Salter
P. australasica Schldl.
P. capitata L.f. = *P. ensifolia*
P. candicans Eckl. & Zeyh. = *Otholobium candicans*
P. cinerea Lindl. = *Cullen cinereum*

P. corylifolia L., as *Cullen corylifolia*
P. cordata Thunb. = *P. monophylla*
P. decumbens Aiton = *Otholobium decumbens*
P. ensifolia (Houtt.) Merr., as *P. capitata*
P. eriantha Benth.
P. esculenta Pursh = *Pediomelon tenuiflorum* (Pursh) Rydb.
P. glandulosa L. = *Otholobium fruticans* (L.) C.H. Stirton.
P. imbricata (L.f.) T.M. Salter
P. laxa T.M. Salter
P. monophylla (L.) C.H. Stirt., as *P. cordata*
P. obtusifolia DC. = *Cullen obtusifolium*
P. oligophylla Eckl. & Zeyh.
P. onobrychis Nutt. = *Orbexillum onobrychis* (Nutt.) Rydb.
P. orbicularis Lindl. = *Hoita orbicularis* (Lindl.) Rydb.
P. patens Lindl. = *Cullen patens*
P. pinnata L.
P. plumosa F. Muell.
P. psoralioides (Walter) Cory = *Orbexilum pedunculatum* var. *gracile* (Torr. & A. Gray) J.W. Grimes
P. pustulata F. Muell.
P. ramulosa auct. Yates et al., pers. comm. (2008)
P. repens P. Bergius
P. restioides Eckl. & Zeyh.
P. rotundifolia L. = *Otholobium rotundifolium*
P. simplex Torr. & A. Gray = *Orbexilum simplex* (Nutt. ex Torr. & A. Gray) Rydb.
P. tenax Lindl. = *Cullen tenax*
P. tenuiflora Pursh = *Psoralidium tenuiflrum* (Pursh) Rydb.
P. tomentosa Thunb. = *Otholobium sericeum*
P. verracosa Willd.
P. wilmsii Harms = *Otholobium wilmsii*

Psoralidium

P. argophyllum (Pursh) Rydb.
P. tenuiflorum (Pursh) Rydb.

Psorothamnus

P. emoryi (A. Gray) Rydb.
P. schottii Torr.) Barneby
P. scoparius (A. Gray) Rydb.
P. spinosus (A. Gray) Rydb., as *Dalea spinosa* (A. Gray)

Pterocarpus

P. acapulcensis Rose, as *P. podocarpus*
P. angolensis DC.
P. antunesii (Taub.) Harms
P. brenanii L. Barbosa & Torre
P. echinatus Pers.
P. erinaceus Poir.
P. indicus Willd.
P. lucens Lepr.
P. macrocarpus
P. marsupium Roxb.
P. mildbraedii Harms subsp. *mildbraedii* Diabate et al. (2005).
P. officinalis Jacq.
P. osun Craib
P. podocarpus Blake = *P. acapulcensis*
P. rotundifolius (Sond.) Druce and var. *martinii* (Dunkley) Mendonca & Sousa and subspp. *polyanthus* (Harms) Mendonca & Sousa and *rotundifolius* (Sond.) Druce
P. santalinoides DC.
P. santalinus L.f.
P. soyauxii Taub.
P. vidalianus Rolfe

Ptycholobium

P. biflorum subsp. *biflorum* (E. Mey.) Brummitt
P. contortum (N.E. Br.) Brummitt
P. plicatum (Oliv.) Harms

Pueraria

P. lobata (Willd.) Ohwi = *P. montana* var *lobata* (Willd.) Sanjappa & Predeep
P. montana (Lour.) Merr.
P. phaseoloides (Roxb.) Benth.
P. thomsonii Benth. = *P. lobata* subsp. *thomsonii*
P. tuberosa (Roxb. ex Willd.) DC.
P. wallichii DC.

Pultenaea

P. acerosa R.Br.
P. altissima F. Muell.
P. blakelyi J. Thompson
P. canaliculata F. Muell.
P. capitellata DC.
P. daphnoides Wendl.
P. densifolia F. Muell.
P. elliptica Sm. = *P. tuberculata*
P. ericifolia Benth.
P. involucrata Benth.
P. largiflorens Benth. var. *latifolia* H.B. Will.
P. laxiflora Benth. var. *pilosa* H.B. Will.
P. microphylla Siebold
P. myrtoides A. Cunn. ex Benth.
P. obovata Benth. = *altissima*
P. ochreata Meisn.
P. paleacea Willd.
P. procumbens A. Cunn.
P. prostrata Benth.
P. reticulata (Sm.) Benth.
P. retusa Sm.
P. scabra R.Br.
P. stipularis Sm.

P. strobilifera Meisn.
P. tenuifolia R.Br.
P. teretifolia Williams var. *brachyphylla* Williams.
P. tuberculata Pers.
P. verruculosa Turcz.
P. villosa Willd.

Pycnospora

P. lutescens (Poir.) Schindl.

Rafnia

R. acuminata (E. Mey.) G.J. Campb. & B-E van Wyk
R. amplexicaulis Thunb.
R. angulata Thunb.
R. capensis (L.) Schinz and sspp. *capensis* and *ovata*
R. crassifolia Harv.
R. cuneifolia Thunb.
R. diffusa Thunb. Yates et al., pers. comm. (2008)
R. elliptica Thunb.
R. globosa G.J. Campbell & B.-E. van Wyk R. Yates et al. pers. comm. (2008)
R. opposita Thunb.
R. ovata E. Mey.
R. perfoliata E. Mey.
R. racemosa Eckl. & Zeyh.
R. triflora Thunb.

Ramirezella

R. strobilophora (Robinson) Rose

Requiena

R. pseudosphaerosperma (Schinz)
R. sphaerosperma DC.

Retama

R. monosperma (L.) Boiss.
R. raetam (Forssk.) Webb, as *Lygos raetam* subsp. *raetam* (Forssk.) Heyw.
R. sphaerocarpa (L.) Boiss.

Riedeliella

R. graciflora Harms

Rhynchosia

R. adenodes Eckl & Zeyh., as *R. effusa*
R. albissima Gand.
R. angulosa Schinz
R. aurea (Willd.) DC. H.S. Gehlot, pers. com. (2007)
R. brunnea Baker f. Diabate et al. (2005)
R. buchananii Harms
R. capensis (Burm.f.) Schinz
R. caribaea (Jacq.) DC. and var. *picta* (E. Mey.) Baker f.
R. ciliata (Thunb.) Druce
R. clivorum S. Moore
R. confusa Burtt Davy
R. cooperi (Baker f.) Burtt Davy
R. cunninghamii Benth.
R. densiflora (Roth) DC. and subsp. *chrysadenia* (Taub.)Verdc.
R. divaricata Baker
R. diversifolia Micheli Real et al. (2005)
R. effusa Druce = *R. adenodes*
R. elegantissima Schinz = *R. totta*
R. erecta (Walt.) DC. = *R. tomentosa*
R. ferulifolia Harv. Garau et al. (2009)
R. fleckii Schinz
R. goetzei Harms
R. harvei Eckl. & Zeyh.
R. himalensis Baker
R. hirsuta Eckl. & Zeyh.
R. hirta (Andrews) Meikle & Verdc.
R. holosericea Schinz
R. holstii Harms
R. hosei Griseb.
R. insignis (O. Hoffm.) R.E.Fr.
R. jacottetii Schinz = *R. reptabunda*
R. komatiensis Harms
R. luteola (Hiern) Schum.
R. memnonia DC. = *R. minima*
R. minima (L.) DC. and vars. *minima* (L.) DC. and *prostrata* (Harv.) Meikle
R. mollissima (Ell.) Shuttlew. ex W. Watson = *R. tomentosa* var. *mollissima*
R. monophylla Schltr.
R. namaensis Schinz.
R. nervosa Harv. and var. *petiolata* Burtt Davy
R. nitens Harv.
R. nyasica Baker
R. parviflora E. Mey.
R. pentheri A. Zahlbr. vars. *hutchinsoniana* Burtt Davy and *pentheri* Schltr.
R. phaseoloides (Sw.) DC.
R. procurrens (Hiern.) Schum. subsp. *floribunda* (Baker) Verdc.
R. pseudo-cajan Cambess.
R. pulverulenta Stocks
R. pycnostachya (DC.) Meikle
R. pyramidalis (Lam.) Urb.
R. reptabunda N.E. Br.
R. resinosa (A. Rich.) Baker
R. reticulata (Sw.) DC.
R. rothii Aiton
R. rufescens (Willd.) DC.
R. schimperi Boiss. H.S. Gehlot, pers. comm. (2007)
R. senna Hook. & Arn. and var. *texana* (Torr. & A. Gray) M. Johnst., as *R. texana*
R. sordida (E. Mey.) Schinz
R. stipata Meikle
R. sublobata (Schum.) Meikle
R. swynnertonii Baker f.
R. texana Torr. & A. Gray = *R. senna* var. *texana* (Torr. & A. Gray) M.C. Johnst.

R. thorncroftii (Baker f.). Burtt Davy
R. tomentosa (L.) Hook. & Arn., as *R. erecta* and var. *mollissima* (Elliott) Torr. & A. Gray, as *R. mollissima*
R. totta (Thunb.) DC. and vars. *totta* DC. and *venulosa* (Hiern) Schum.
R. tricuspidata Baker f.
R. venulosa (Hiern) Schum. = *R. senna* var. *texana*
R. villosa (Meisn.) Druce, as *Eriosema villosum*
R. volubilis Lour.

Robinia

R. hispida L. and var. *kelseyi* (Hutch.) Isely, as *R. kelseyi*
R. pseudoacacia L.
R. viscosa Vent.

Robynsiophyton

R. vanderystii R. Wilczek

Rothia

R. hirsuta (Guill. & Perr.) Baker
R. indica (L.) Druce

Scorpiurus

S. muricatus L. and var. *subvillosus* (L.) Fiori
S. vermiculatus L.

Securigera

S. cretica (L.) Lassen, as *Coronilla cretica*
S. orientalisI (Mill.) Lassen, as *Coronilla cappadocica*
S. securidaca (L.) Degen & Doefler
S. varia (L.) Lassen, as *Coronilla varia*

Sesbania

S. aculeata Poir. = *S. bispinosa*
S. aegyptica Poir. = *S. bispinosa*
S. benthamiana Domin
S. bispinosa (Jacq.) W. Wright
S, brachycarpa F. Muell.
S. brevipedunculata J.B. Gillett
S. cannabina (Retz.) Pers.
S. canavillesii S. Wats. = *S. longiflora*
S. cinerascens Baker
S. cochinchinensis (Lour.) DC. = *S. javanica*
S. coerulescens Harms
S. concolor J.B. Gillett
S. drummondii (Rydb.) Cory
S. emerus (Aubl.) Urb.
S. erubescens (Benth.) N. Burb.
S. exaltata (Raf.) Cory
S. formosa (F. Muell.) N. Burb.
S. grandiflora (L.) Pers.
S. greenwayi J.B. Gillett
S. herbacea (Mill.) McVaugh, as *S. macrocarpa*
S. javanica Miq., as *S. cochinchinensis*
S. leptocarpa DC.
S. longifolia DC.
S. macrantha E. Phillips & Hutch.
S. macrocarpa = *S. exaltata*
S. macroptera Micheli
S. microphylla E. Phillips & Hutch.
S. mossambicensis Klotzsch subsp. *mossambicensis* Klotzsch
S. pachycarpa DC.
S. punicea (Cav.) Benth.
S. punctata DC. – *S. sesban*
S. rogersii E. Phillips & Hutch. = *S. tetraptera* subsp. *rogersii*
S. rostrata Bremek. & Oberm.
S. roxburghii Merr. = *S. javanica*
S. sericea (Willd.) Link
S. sesban (L.) Merr. and vars. *muricata* Baquar, *nubica* Chiov. and *zambesiaca* J.B. Gillett
S. sonorae Taub.
S. speciosa Taub.
S. sphaerosperma Welw.
S. tetraptera Baker subsp. *rogersii* (E. Phillips & Hutch.) G.P. Lewis, as *S. rogersii*
S. tomentosa Hook. & Arn.
S. transvaalensis J.B. Gillett
S. tripettii (Poir.) Hort. ex F.T. Hubb. = *S. punicea*
S. vesicaria (Jacq.) Elliott
S. virgata (Cav.) Pers.

Shuteria

S. densiflora Benth.
S. vestita Wight & Arn. = *S. involucrata*
S. involucrata (Wall.) Wight & Arn.

Smirnowia

S. turkestana Bunge

Smithia

S. begimina Dalz.
S. blanda Wallich
S. ciliata Royle
S. capitata Dalz.
S. conferta Sm.
S. erubescens (E. Mey.) Baker f.
S. eylesii S. Moore
S. purpurea Kunth.
S. pycnantha Benth.
S. salsuginea Hance
S. sensitiva Aiton
S. setulosa Dalz.

Sophora

S. alopecuroides L.
S. angustifolia Siebold & Zucc. = *S. flavescens*
S. chrysophylla (Salisb.) Seeman
S. davidii (Franch.) Pavol., also as *S. viciifolia*
S. flavescens Aiton, also as *S. angustifolia*
S. formosa Kearn. & Peeb. = *Calia. arizonica* (S. Watson) Yakovlev
S. gypsophila B. Turner & Powell var. *guadalupensis* B. Turner & Powell
S. howinsula (Oliv.) P. Green
S. inhambanensis Klotzsch
S. microphylla Aiton
S. mollis (Royle) Baker subsp. *griffithii* (Stocks) Ali
S. moorcroftiana Benth.
S. prostrata Buchanana
S. secundiflora (Ortega) DC. = *Calia aecundiflora* (Ortega) Yakovlev
S. tetraptera J.F. Mill.
S. tomentosa L.
S. velutina Lindl. subsp. *zimbabweensis* J.B. Gillett & Brummitt
S. viciifolia Hance = *S. davidii*

Spartium

S. junceum L.

Spatholobus

S. harmondii Gagnep.
S. parviflorus (Roxb. ex DC.) Kuntze

Sphaerolobium

S. alatum Benth.
S. grandiflorum (R.Br.) Benth.
S. medium R.Br.

Sphaerophysa

S. salsula (Pall.) DC.

Sphenostylis

S. angustifolia Sonder
S. erecta (Baker f.) Hutch. ex Baker f.
S. marginata E. Mey.
S. stenocarpa (A. Rich.) Harms

Stauracanthus

S. genistoides (Brot.) Samp.

Strongylodon

S. lucidus (G. Forst.) Seem.
S. macrobotrys A. Gray
S. ruber Vogel

Strophostyles

S. helvola Elliott and var. *missouriensis* Britton
S. leiosperma (Torr. & A. Gray) Piper
S. pauciflorus (Benth.) S. Watson = *S. leiosperma*
S. umbellata (Willd.) Britton

Stylosanthes

S. angustifolia Vogel
S. biflora (L.) Britton et al.
S. bojeri Vogel = *S. fruticosa*
S. bracteata Vogel
S. calcicola Small
S. capitata Vogel
S. debilis M.B. Ferreria & Sousa Costa
S. erecta P. Beauv.
S. fruticosa (Retz.) Alston
S. gracilis Kunth = *S. guianensis*
S. guianensis (Aubl.) Sw. and subsp. *guianensis* (Aubl.) Sw.
S. hamata (L.) Taub.
S. humilis Kunth
S. leiocarpa Vogel
S. linearifolia M.B. Ferreria & Sousa Costa
S. macrocephala M.B. Ferreira & S. Costa
S. mexicana Taub.
S. montividensis Vogel
S. mucronata Willd. = *S. fruticosa*
S. pilosa M.B. Ferreria & Sousa Costa
S. riparia Kearn = *S. biflora*
S. ruelloides Mart. ex Benth.
S. scabra Vogel
S. sundaica Taub. = *S. humilis*
S. tomentosa Taub.
S. tuberculata S.F. Blake = *S. scabra*
S. viscosa Sweet

Sulla

S. capitata B.H. Choi & H. Ohasi, as *Hedysarum capitatum*
S. carnosa (Desf.) B.H. Choi & H. Ohasi, as *H. carnosum*
S. coronaria (L.) B.H. Choi & H. Ohasi, as *H. coronarium*
S. flexuosa (L.) B.H. Choi & H. Ohasi, as *H. flexuosum*
S. glomerata (F. Dietr.) B.H. Choi & H. Ohasi, as *H. glomeratum*
S. pallida (F. Dietr.) B.H. Choi & H. Ohasi, as *H. pallida*
S. spinosissima (L.) B.H. Choi & H. Ohasi, as *H. spinosissima*

Sutherlandia

S. frutescens (L.) R.Br.

Swainsona

S. burkittii Benth.
S. calcicola Joy Thomps.
S. campylantha F. Muell.
S. canescens F. Muell.
S. fissimontana J. Black
S. flavicarinata J. Black
S. forrestii F. Muell. ex A.T. Lee
S. galegifolia (Andrews) R. Br.
S. greyana Lindl.
S. incei W.R. Price
S. kingii F. Muell.
S. lessertiifolia DC.
S. maccullochiana F. Muell.
S. microphylla Gray
S. novae-zelandiae Hook. f., = *Montigena novae-zelandiae*
S. occidentalis F. Muell. = *S. pterostylis*
S. oroboides Benth. subsp. *oroboides* F. Muell.
S. phacoides Benth. subsp. *phacoides* Benth.
S. procumbens F. Muell.
S. pterostylis (DC.) Bakh. f.
S. rigida J. Black
S. stipularis F. Muell.
S. swainsonioides (Benth.) A. Lee

Swartzia

S. acutifolia Vogel
S. apetala Raddi
S. arborescens (Aubl.) Pittier
S. auriculata (Poepp.) Endl.
S. bahiensis Cowan
S. bannia Sandwith
S. benthamiana Miq.
S. caribaea Griseb.
S. flaemingii Raddi
S. glazioviana (Taub.) Glaz.
S. grandifolia Benth.S.M. de Faria pers. comm. to J.H. Kirkbride (2006)
S. guianensis Aubl.
S. jenmanii Sandwith
S. laevicarpa Amshoff.
S. langsdorffii Raddi
S. laurifolia Benth.
S. laxifolia Bong ex Benth.
S. leiocalycina Benth.
S. macrostachya Benth.
S. madagascariensis Desv. = *Bobgunnia madagascariensis* (Desv.) J.H. Kirkbr. & Wiersema.
S. oblanceolata Sandwith
S. oriximinaensis R.S. Cowan S.M. de Faria pers. comm. to J.H. Kirkbride (2006)
S. panacoco (Aubl.) Cowan
S. pinnata (Vahl) Willd.
S. polyphylla (DC.)
S. schomburgkii Benth.
S. simplex (Sweet) Spreng.
S. trinitensis Urb.

Syrmatium

S. cytisoides (Benth.) Greene, as *Lotus cytisoides*
S. decumbens (Benth.) Greene
S. glabrum Vogel, as *L. scoparius*
S. junceum Greene, as *L. junceus*
S. nevadense Greene, as *L. nevadensis* (S. Watson) Greene = *S. decumbens*

Tadehagi

T. triquetrum (L.) H. Ohashi, as *P. triquetrum* (DC.) Benth. and subsp. *auriculatum* (DC.) H. Ohashi, as *P. auriculatum* (DC.) Schindl.

Taverniera

T. cuneifolia Arn.
T. lappacea (Forssk.) DC.

Templetonia

T. retusa (Vent.) R.Br.
T. sulcata (Meisn.) Benth.

Tephrosia

T. acaciaefolia Baker
T. adunca Benth.
T. aemula (E. Mey.) Harv.
T. aequilata Baker subspp. *australis* Brummitt and *nyasae* (Baker f.) Brummitt, as *T. zombensis*
T. apollina (Delile) Link
T. baueri (A. Gray)
T. bidwilli Benth.
T. biflora E. Mey. = *Ptycholobium biflorum* subsp. *biflorum* (E. Mey.) Brummitt
T. brachyodon Domin
T. bracteolata Guill. & Perr.
T. burchellii Burtt Davy
T. candida (Roxb.) DC.
T. capensis (Jacq.) Pers. and vars. *acutifolia* E. Mey. and *hirsuta* Harv.
T. cathartica Sessé & Moçino = *T. senna*
T. cephalantha Baker var. *decumbens* Baker
T. chimanimaniana Brummitt
T. cinerea (L.) Pers.
T. contorta N.E. Br., also as *Ptycholobium contortum* (N.E. Br.) Brummitt
T. cordata Hutch. & Burtt Davy
T. coronilloides Baker
T. dasyphylla Baker subsp. *dasyphylla* Baker
T. decora Baker
T. dichotoma Desv. = *T. pumila* (Lam.) Pers.
T. dietrichiae Domin
T. dregeana E. Mey.
T. elata Defl. subsp. *elata* Defl.
T. elongata E. Mey., as *T. tzaneenensis* and vars. *elongata*, E. Mey. *lasicaulos* Brummitt and *pubescens* Harv.
T. euchroa Verdc.
T. festina Brummitt
T. filipes Benth.

T. forbesii Baker subsp. *interior* Brummitt
T. flagellaris Domin.
T. glomeruliflora Meisn. and subsp. *meisneri* (Hutch. & Burtt Davy) B.D. Schrire, as *T. grandibracteata* Merxm.
T. grandiflora (Aiton) Pers.
T. heckmanniana Harms, as *T. elata* subsp. *heckmanniana*
T. hookeriana Wight & Arn.
T. incarnata Brummitt = *T. glomeruliflora* subsp. *meisneri*
T. juncea Benth.
T. linearis (Willd.) Pers. var. *linearis* (Willd.) Pers.
T. longipes Meisn. subsp. *swynnertonii* (Baker f.) Brummitt
T. lupinifolia DC., also as *Lupinophyllum lupinifolia* (DC.) Gillett
T. lurida Sonder and vars. *drummondii* Brummitt and *lurida* Sonder = *T. longipes*
T. macropoda (E. Mey.) Harv.
T. maxima (L.) Pers.
T. micrantha J.B. Gillett
T. montana Brummitt
T. multijuga R.G. Young
T. natalensis H.M. Forbes subsp. *pseudocapitata* (H.M. Forbes) B.D. Schrire, as *T. pseudocapitata*
T. nitens Benth. ex Seem. S.M. de Faria pers. comm. to J.H. Kirkbride (2006)
T. noctiflora Baker
T. obovata Merr.
T. pallens Aiton
T. paniculata Baker var. *paniculata* Baker
T. paradoxa Brummitt
T. plicata Oliver, = *Ptycholobium plicatum* (Oliv.) Harms
T. polystachya E. Mey. and vars. *hirta* Harv. and *latifolia* Harv.
T. praecana Brummitt
T. pseudocapitata H.M. Forbes = *T. natalensis* subsp. *pseudocapitata* (H.M.L. Forbes) Schrire
T. pseudosphaerosperma Schinz = *Requienia pseudosphaerosperma* (Schinz) Brummitt
T. pumila var. *pumila* (Lam.) Pers.
T. purpurea (L.) Pers. subspp. *altissima* Brummitt and *leptostachya* (DC.) Brummitt vars. *delagoensis* (H.M. Forbes) Brummitt and *pubescens* (Baker) Brummitt
T. radicans Baker
T. reptans Baker and var. *reptans* Baker
T. rhodesica Baker f. and vars. *evansii* (Hutch. & Burtt Davy) Brummitt, *polystachyoides* (Baker f.) Brummitt and *rhodesica* Baker f.
T. rigida Baker = *T. elata* Doignon-Bourcier et al. (1999)
T. rosea F. Muell. ex Benth.
T. rufula Pedley
T. rupicola J.B. Gillett
T. semiglabra Sonder
T. senna Kunth, as *T. cathartica*
T. sessiliflora (Poir.) Hassl.
T. shiluwanensis Schinz
T. sinapou (Buc'hoz) A. Chev., as *T. toxicana*
T. sparsiflora H.M. Forbes
T. sphaerosperma DC., = *Requienia sphaerosperma* DC.
T. sphaerosphora F. Muell.
T. spicata (Walter) Torr. & A. Gray
T. stormsii var *stormsii* de Wild.
T. stricta (L.f.) Pers.
T. strigosa (Dalzell) Sant. & Maheshw.
T. subtriflora Baker
T. subulata Hutch. & Burtt Davy
T. supina Domin
T. tenella A. Gray = *T. vicioides*
T. tenuis Wall.
T. toxicana (Sweet) Pers. = *T. sinapou*
T. tzaneenensis H.M. Forbes = *T. elongata*
T. uniflora ssp *uniflora* Pers.
T. vestita Vogel
T. vicioides Schldtl.
T. villosa (L.) Pers. and subsp. *ehrenbergiana* (Schweinf.) Brummitt
T. virginiana (L.) Pers.
T. vogelii Hook. f.
T. zombensis Baker = *T. aequilata* subsp. *nyasae* (Baker f.) Brummitt
T. zoutpansbergensis Brem.

Teramnus

T. labialis (L.f.) Spreng. and var. *abyssinicus* (A. Rich.) Verdc.
T. repens (Taub.) Baker f.
T. uncinatus (L.) Sweet and subsp. *ringoetii* (De Wild.) Verdc.
T. volubilis Sweet

Tetragonolobus

T. maritimus (L.) Roth
T. palestinus Boiss.
T. purpureus Moench
T. subpinnata Torr. & A. Gray = *Acmispon wrangelianus*

Teyleria

T. koordersii (Backer) Backer

Thermopsis

T. barbata Benth.
T. caroliniana M.A. Curt. = *T. villosa*
T. fabacea (Pallas) DC. = *T. lupinoides*
T. inflata Cambess.
T. lanceolata R.Br.
T. lupinoides (L.) Link
T. macrophylla Hook. & Arn.
T. montana Nutt.
T. rhombifolia (Pursh) Richardson and var. *montana* (Torr. & A. Gray) Isely = *T. montana* var. *montana*
T. villosa (Walter) Fern. & B.G. Schubert, as *T. carolininana*

Tibetia

T. himalaica (Baker) H.P. Tsui, as *Gueldenstaedtia himalaica*

Tipuana

T. tipu (Benth.) Kuntze

Trifolium

T. affine C. Presl
T. africanum Ser.
T. agrarium L. = *T, aureum*
T. albopurpureum Torr. & A. Gray
T. alexandrinum L.
T. alpestre L.
T. alpinum L.
T. amabile Kunth.
T. ambiguum M. Bieb.
T. amphianthum Torr. & A. Gray = *T. polymorphum*
T. angustifolium L.
T. opertum Bobrov
T. argutum Banks & Sol., as *T. xerocephalum*
T. arvense L.
T. aureum Pollich
T. baccarinii Chiov.
T. badium Schreb.
T. barbigerum Torr.
T. beckwithii S. Watson
T. bejariense Moric.
T. berytheum Boiss. & Blanche
T. bifidum A. Gray
T. bocconei Savi
T. boissieri Guss.
T. brandegei S. Watson
T. burchellianum Ser. and subsp. *johnstonii* (Oliv.) J.B. Gillett
T. campestre Schreb., also as *T. agrarium*
T. canescens Willd.
T. carmeli Boiss. = *T. echinatum* var. *carmeli* (Boiss.) Gibelli & Belli
T. carolinianum Michx.
T. cernum Brot.
T. cheranganiense J.B. Gillett
T. cherleri L.
T. ciliolatum Benth.
T. clusii Godr. & Gren.
T. clypeatum L.
T. compactum Post = *T. lucanicum*
T. cryptopodium A. Rich.
T. cyathiferum Lindl.
T. dalmaticum Vis.
T. dasyurum C. Presl, also as *T. formosum*
T. decorum Chiov.
T. depauperatum Desv. and var. *amplectens* (Torr. & A. Gray) S. Watson, as *T. stenophyllum*
T. desvauxii Boiss & Blanche = *T. purpureum*
T. dichotomum Hook. & Arn.
T. diffusum Ehrh.
T. dubium Sibth., also as *T. procumbens* and *T. filiforme*
T. echinatum M. Bieb., as *T. supinum* and var. *carmeli* (Boiss.) Gibelli & Belli, as *T. carmeli*
T. elegans Savi = *T. hybridum* subsp. *elegans*
T. expansum Waldst. & Kit. = *T. pratense* var. *americanum*
T. filiforme L. = *T. micranthum*
T. flavulum Greene = *T. fucatum*
T. formosum d'Urv. = *T. dasyurum*
T. fragiferum L.
T. fucatum Lindl., also as *T. flavulum*
T. glanduliferum Boiss.
T. globosum L.
T. glomeratum L.
T. gracilentum Torr. & A. Gray
T, grandiflorum Schreb., as *T. speciosum*
T. haydenii Porter
T. heterodon A. Gray = *T. wormskioldii*
T. hirtum All.
T. hybridum L. and subsp. *elegans* (Savi) Asch. & Graebner, as *T. elegans*
T. incarnatum L.
T. isodon Murb. = *T. obscurum*
T. isthmocarpum Brot.
T. involucratum Ortega = *T. willdenovii* or *T. mucratum* subsp. *mucratum**
T. johnstonii Oliv. = *T. semipilosum*
T. kingii S. Watson and subsp. *productum* (Greene) D. Heller
T. lappaceum L.
T. leucantium M. Bieb.
T. ligusticum Lois.
T. longipes Nutt. (= *T. longipes* Torr. & A. Gray?)
T. lucanicum Guss., as *T. compactum*
T. lupinaster L.
T. maritimum Huds. = *T. squamosum*
T. masaiense J.B. Gillett
T. mattirolianum Chiov.
T. medium L.
T. meduseum Boiss.

T. melananthum Hook. & Arn. = *T. variegatum*
T. meneghinianum Clementi = *T. nigrescens* subsp. *petrisavii*
T. michelianum Savi
T. micranthus Viv.
T. microcephalum Pursh
T. microdon Hook. & Arn.
T. miegeanum Maire
T. montanum L.
T. mucronatum Spreng. subsp. *mucronatum* Spreng., as *T. involucratum*
T. mutabile Port.
T. nanum Torr.
T. nigrescens Viv. and subsp. *petrisavii* (Clementi) Holmboe, as *T. meneghianum,* and as *T. petrisavi*
T. obscurum Savi, as *T. isodon*
T. occidentale Coombe = *T. repens* var. *soletti* (Dted. & Hochst.) Asch. & Graebn.
T. ochroleucum Huds.
T. oliganthus Steud.
T. ornithopodioides (L.) Sm., as *Trigonella ornithopodioides*
T. palaestinum Boiss.
T. pallescens Schreb.
T. pallidum Waldst. & Kit.
T. pannonicum Jacq.
T. petrisavi Clem. = *T. nigrescens* subsp. *petrisavi*
T. parryi A. Gray
T. parviflorum F.E. Ehrh. = *T. retusum*
T. patens Schreb.
T. pauciflorum d'Urv.
T. philistaeum Zohary
T. physodes Steven ex M. Bieb.
T. pilulare Boiss.
T. plebeium Boiss.
T. polymorphum Poir., also as *T. amphianum* and *T. nivale* Arv.-Touv
T. polystachyum Fresen.
T. pratense L. and vars. *americanum* Harz, and *sativum* Scheib.
T. procumbens L. = *T. dubium*
T. pseudostriatum Baker f.
T. purpureum Lois., also as *T. desvauxii*
T. reflexum L.
T. repens L.
T. resupinatum L.
T. retusum L., as *T. parviflorum*
T. rubens L.
T. rueppellianum Fresen.
T. rusbyi Greene subsp. *reflexum* (Nelson) D. Heller & Zohary, as *T. rydbergii*
T. rydbergii Greene = *T. rusbyi* subsp. *reflexum*
T. scabrum L.
T. scutatum Boiss.
T. semipilosum Fresen., also as *T. johnstonii* and vars. *glabrescens* J.B. Gillett, *kilimanjaricum* Baker f. and *semipilosum* Fresen.
T. simense Fresen.
T. somalense Taub.
T. spadiceum L.
T. speciosum Willd. = *T. grandiflorum*
T. spumosum L.
T. squamosum L., also as *T. maritimum*
T. squarrosum L.
T. stellatum L.
T. stenophyllum Boiss. = *T. depauperatum* var. *stenophyllum*
T. steudneri Schweinf.
T. stoloniferumI Muh. ex Eaton
T. striatum subsp. *brevidens* Lange
T. strictum L.
T. subterraneum L. and subspp. *brachycalycium* Katzn. & Morley, *subterraneum* L. and *yanninicum* Katzn. & Morley
T. suffocatus L.
T. supinum Savi = *T. echinatum*
T. tembense Fresen.
T. thalii Vill.
T. tomentosum
T. tridentatum Lindl. = *T. willdenovii*
T. tumens Steven ex M. Bieb.
T. uniflorum L.
T. usambarense Taub.
T. variegatum Torr. & A. Gray
T. vavilovii Eig
T. vernum Phil.
T. vesiculosum Savi
T. willdenovii Spreng., as *T. involucratum* and as *T. tridentatum*
T. wormskioldii Lehm., as *T. heterodon* and possibly as *T. involucratum**
T. xerocephalum Fenzl = *T. argutum*

* The naming of *T. involucratum* as used in Allen & Allen (1981) could refer to more than one currently accepted species; all known possibilities have been included here.

Trigonella

T. anguina Delile
T. arabica Delile
T. archiducis-nicolai (Sirj.) Vassilcz = *Medicago archducis-nicolai*
T. arcuata C. Mey., = *Medicago medicaginoides*
T. aurantiaca Boiss. = *Medicago phrygia*
T. balansae Boiss. & Reuter, also as *T. corniculata* (L.) L.
T. berthyea Boiss. & Blanche
T. caerulea (L.) Ser.
T. calliceras M. Bieb.
T. cancellata Pers., = *Medicago medicaginoides*
T. coelesyriaca Boiss.
T. corniculata (L.)L.
T. cretica (L.) Boiss.
T. cylindracea Desv.

T. emodi Benth.
T. foenum-graecum L.
T. geminiflora Bunge
T. glabra Thunb., as *T. hamosa* and subsp. *uncata* (Boiss. & Noë) Lassen
T. gladiata M. Bieb.
T. gracilis Benth.
T. hamosa L. = *T. hierosolymitana*
T. hierosolymitana Boiss.
T. hybrida Pourr. = *Medicago hybrida*
T. monantha C. Mey. = *Medicago monantha*
T. monspeliaca L. = *Medicago monspeliaca*
T. occulta Ser.
T. ornithopodioides (L.) DC. = *Trifolium ornithopodioides*
T. orthoceras Kar. & Kir.) = *Medicago orthoceras*
T. stellata Forssk.
T. suavissima Lindl.
T. verae Sirj.

Tripodion

T. tetraphyllum (L.) Fourr., as *Physanthyllis tetraphylla* (L.) Boiss. and *Anthyllis tetraphylla* L.

Ulex

U. europaeus L.
U. gallii Planchon

Uraria

U. crinita (L.) DC.
U. cylindracea Benth.
U. lagopodioides (L.) DC.
U. neglecta Prain
U. picta (Jacq.) DC.
U. rufescens Schindl.
U. spinosa Desv.

Vandasina

V. retusa (Benth.) Rauschert

Vavolovia

V. formosa (Steven) Al Fed.

Vicia

V. acutifolia Elliott
V. alba Moench = *V. sativa* subsp. *sativa*
V. americana Willd.
V. amoena Fisch.
V. amphicarpa L. = *V. sativa* subsp. *amphicarpa*
V. amurensis Oett.
V. angustifolia L. = *V. sativa* subsp. *nigra*
V. articulata Hornem.
V. baborensis Batt. & Trab. = *V. ochroleuca* subsp. *baborensis*
V. baicalensis (Turcz.) Fedtsh. = *V. venosa*
V. bakeri Ali
V. benghalensis L.
V. benthamiana Ali
V. biennis L.
V. bithynica (L.) L.
V. bungei Ohwi
V. caroliniana Walter
V. cassubica L.
V. cordata Wulf. = *V. sativa* subsp. *cordata*
V. cracca L.
V. dasycarpa Ten. = *V. villosa* subsp. *varia*
V. disperma DC.
V. dumetorum L.
V. ervilia (L.) Willd.
V. exigua Nutt. = *V. ludoviciana* subsp. *ludoviciana*
V. faba L. and var. *equina* Pers.
V. ferruginea Boiss.
V. floridana S. Watson
V. fulgens Batt.
V. graminea Sm.
V. grandiflora Scop.
V. hirsuta (L.) Gray
V. hybrida L.
V. hyrcanica Fisch. & Mey.
V. lathyroides L.
V. laxiflora Brot. = *V. parviflora*
V. leavenworthii Torr. & A. Gray = *V. ludoviciana* ssp *leavenworthii*
V. ludoviciana Torr. & A. Gray and subspp. *leavenworthii* (Torr. & A. Gray) J.S. Lassetter & Gunn, as *V. leavenworthii* and *ludoviciana* Torr. & A. Gray, as *V. exigua*
V. lutea L. and subsp. *vestita* (Boiss.) Rouy
V. macrocarpa Bert. = *V. sativa* subsp. *macrocarpa*
V. melanops Sibth. & Sm.
V. micrantha Nutt. = *V. minutiflora*
V. minutiflora D. Dietr., as *V. micrantha*
V. monantha Retz.
V. montevidensis Vogel
V. narbonensis L.
V. nipponica Matsum.
V. noeana Boiss.
V. obscura Vogel = *V. montevidensis*
V. ochroleuca Ten. subsp. *baborensis* (Batt. & Trab.) Greuter & Burdet, as *V. baborensis*
V. palaestina Boiss.
V. pannonica Crantz
V. parviflora Cav., as *V. tenuissima*
V. peregrina L.
V. pisiformis L.
V. pseudorobus Fisch. & C.E. Mey. Herrmann (1994)
V. pubescens (DC.) Link
V. ramuliflora (Maxim.) Ohwi
V. rigidula Royle
V. sativa L. and subspp. *amphicarpa* (Dorthes) Asch. & Graebner, as *V. amphicarpa*; *cordata* (Hoppe) Asch. & Graebn., as *V.*

cordata; *macrocarpa* (Moris) Arcang., as *V. macrocarpa*; *nigra* (L.) Ehrh., as *V. angustifolia* and *sativa* L., as *V. alba*
V. sepium L.
V. serratifolia Jacq.
V. sicula (Raf.) Guss.
V. silvatica L.
V. tenuifolia Roth
V. tenuissima (Bieb.) Schinz & Thell. = *V. parviflora*
V. tetrasperma (L.) Schreb.
V. unijuga A. Br.
V. venosa (Link) Maxim. Herrmann (1994)
V. villosa Roth and subsp. *varia* (Host) Corb., also as *V. dasycarpa*

Vigna

V. aconitifolia (Jacq.) Maréchal
V. adenantha (G. Mey.) Maréchal et al. as *Phaseolus adenanthus*
V. angularis (Willd.) Ohwi & Ohashi
V. angustifoliolata Verdc. = *V. unguiculata* subsp. *stenophylla*
V. candida (Vell.Conc.) Maréchal et al.
V. capensis Walp. = *V. vexillata*
V. caracalla (L.) Verdc.
V. coerulea Baker = *V. unguiculata subsp. tenuis* (E. Mey) Maréchal et al.
V. comosa Baker subsp. *comosa*
V. cylindrica (L.) Skeels = *V. unguiculata* subsp. *cylindrica* (L.) Verdc.
V. dalzelliana (Kuntze) Verdc.
V. davyi Bolus = *V. vexillata* var. *davyi* (Bolus) B.J. Peinaas
V. decipiens Harv.
V. desmodioides R. Wilczek
V. frutescens A. Rich.
V. gazensis Baker f.
V. glabrescens Maréchal, Mascerpa & Stainier
V. gracilis (Guill. & Perr.) Hook.f.
V. hispida = *V. unguiculata* subsp. *dekindtiana* (Harv.) Maréchal et al.
V. hosei (Craib) Backer
V. juncea Milne-Redh.
V. khandalensis (Santapau) Raghaven & Wadhwa
V. lanceolata Benth.
V. lasiocarpa (Benth.) Verdc., as *Phaseolus lasiocarpa*
V. linearis (Kunth) Maréchal et al., as *Phaseolus linearis*
V. longifolia (Benth.) Verdc.
V. luteola (Jacq.) Benth., also as *V. repens*
V. macrorhyncha (Harms) Milne-Redh. = *Wajira grahamiana* (Wight & Arn.) Thulin & Lavin
V. marina (Burm.) Merr.
V. minima (Roxb.) Ohwi & H. Ohashi
V. monophylla Taub.
V. multinervis Hutch. & Dalziel
V. mungo (L.) Hepper
V. nakashimae (Ohwi) Ohwi & H. Ohashi
V. nigrita Hook f.
V. nervosa Markötter
V. nuda N.E. Br.
V. oblongifolia A. Rich. and vars. *oblongifolia* A. Rich. and *parviflora* (Baker) Verdc.
V. owahuensis Vogel
V. parkeri Baker
V. peduncularis (Kunth) Fawcett & Rendle var. *peduncularis* (Kunth) Fawcett & Rendle, as *Phaseolus peduncularis*
V. pilosa (Willd.) Baker
V. pygmaea R.E. Fries
V. racemosa (G. Don) Hutch. & Dalziel
V. radiata (L.) R. Wilczek
V. repens Baker = *V. luteola*
V. reticulata Hook. f.
V. retusa Walp. = *V. marina*
V. sandwicensis A. Gray
V. stenoloba (Harv.) Burtt Davy
V. stenophylla (Harv.) Burtt Davy = *V. unguiculata* ssp *stenophylla*
V. strobilophora Robinson, = *Ramirezella strobilophora* (Robinson) Rose
V. subterranea (L.) Verdc.
V. trilobata (L.) Verdc.
V. triphylla (Wilczek) Verdc.
V. umbellata (Thunb.) Ohwi & Ohashi
V. unguiculata (L.) Walp. and subspp. *cylindrica* (L.) Eselt., *dekindtiana* (Harms) Verdc., also as *V. hispida*, *sesquipedalis* (L.) Verdc. and *stenophylla* (Harv.) Maréchal et al., as *V. angustifoliolata* and as *V. stenophylla*
V. venulosa Baker Diabate et al. (2005)
V. vexillata (L.) A. Rich., also as *V. capensis* and var. *angustifolia* (Schum.) Baker
V. wilmsii Burtt Davy = *V. oblongifolia*

Viminaria

V. juncea (Schrader) Hoffsgg.

Virgilia

V. capensis (L.) Lam = *V. oroboides* subsp. *oroboides*
V. divaricata Adamson
V. oroboides (P. Bergius) T.M. Salter subsp. *oroboides* (P. Bergius) T.M. Salter, as *V. capensis*

Wiborgia

W. armata (Thunb.) Harvey = *W. mucronata*
W. incurvata E. Mey
W. monoptera E. Mey
W. mucronata (L.f.) Druce
W. obcordata (P. Bergius) Thunb.

Wiborgiella

W. humilis Boatwr. & B-E van Wyk, van Wyk & Sprent unpub. (2008)

Wisteria

W. brachybotrys Siebold & Zucc.
W. chinensis DC. = *W. sinensis* (Sims) Sweet
W. floribunda (Willd.) DC. and var. *alba* DC.
W. frutescens (L.) Poir.
W. sinensis (Sims) Sweet
W. venusta Rehder & Wilson

Xeroderris

X. stuhlmannii (Taub.) Mendonca & Sousa

Xiphotheca

X. elliptica (DC.) A.L. Schutte & B.-E. van Wyk
X. reflexa (Thunb.) A.L. Schutte & B-E van Wyk

Zornia

Z. brasilensis Vogel
Z. capensis Pers. sub sp *capensis*
Z. curvata Mohl.
Z. dyctiocarpa DC.
Z. diphylla Pers.
Z. gibbosa Span.
Z. glabra Desv.
Z. glochidiata DC.
Z. guanipensis Pittier
Z. herbacea Pittier
Z. latifolia Smith var. *latifolia* Smith
Z. linearis E. Mey.
Z. marajoara Huber = *Z. guanipensis*
Z. milneana Mohlenbr.
Z. pratensis Milne-Redh. subsp. *pratensis* Milne-Redh.
Z. reticulata Sm., as *Z. diphylla*

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The full list of genera given in the appendices is not indexed here. All genera listed in tables in Chapter 1 are not indexed, but these can be found in the contents pages. Only taxa of sub-generic status or above are listed comprehensively, whereas bacterial taxa are used as major sub-headings and these can be found in the contents pages.

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